New Lower Cretaceous 'libelluloid' dragonflies (Insecta: Odonata: Cavilabiata) with notes about estimated divergence dates for this group

Günther Fleck, André Nel, Günter Bechly, Xavier Delclòs, Edmund A. Jarzembowski & Robert A. Coram

Abstract

Several new fossil Lower Cretaceous Cavilabiata ('Libelluloidea') are studied. In the Araripelibellulidae, the male of *Araripelibellula martinsnetoi* Nel & Paicheler, *1994, Araripelibellula britannica* n. sp. from the UK and *Rencordulia sinica* n. gen., n. sp. from PR China are described. A further specimen of *Cretaneophya strevensi* Jarzembowski & Nel, 1996 is adding new information on its wing venation. In the Chlorogomphida, *Mesochlorogomphus crabbi* n. gen., n. sp. from the UK and *Hispanochlorogomphus rossi* n. gen., n. sp. from Spain are also described and placed in the new family Mesochlorogomphidae. The estimated divergence dates for the libelluloid dragonflies based on molecular data are disputed on the basis of the fossil record. The Cavilabiata ('Libelluloidea') probably appeared during the Early to Middle Jurassic and greatly diversified during the Early Cretaceous.

Keywords: Insecta, Odonata, Anisoptera, Cavilabiata, Araripelibellulidae, Chlorogomphida, Mesochlorogomphidae n. fam., n. gen., n. sp., Lower Cretaceous, UK, Spain, PR China.

Zusammenfassung

Einige neue fossile Cavilabiata ('Libelluloidea') aus der Unteren Kreidezeit werden untersucht. Innerhalb der Araripelibellulidae werden ein Männchen von *Araripelibellula martinsnetoi* Nel & Paicheler, 1994, *Araripelibellula britannica* n. sp. aus Großbritannien und *Rencordulia sinica* n. gen., n. sp. aus der VR China beschrieben. Ein weiteres Exemplar von *Cretaneophya strevensi* Jarzembowski & Nel, 1996 liefert neue Informationen über deren Flügelgeäder. Innerhalb der Chlorogomphida werden *Mesochlorogomphus crabbi* n. gen., n. sp. aus Großbritannien und *Hispanochlorogomphus rossi* n. gen., n. sp. aus Spanien beschrieben und in die neue Familie Mesochlorogomphidae gestellt. Die auf der Grundlage molekularer Daten geschätzten Aufspaltungsalter für die libelluloiden Großlibellen werden an Hand des Fossilberichtes in Zweifel gezogen. Die Cavilabiata ('Libelluloidea') erschienen vermutlich im Frühen bis Mittleren Jura und erlebten eine umfangreiche Diversifizierung in der Unteren Kreide.

Contents

1. Introduction

The very diverse dragonfly clade Cavilabiata (formerly 'libelluloids') is currently considered as one of the most recently diversified of the suborder Anisoptera, with the oldest known taxa dating from the Middle to Late Jurassic (Aeschnidiidae, Nannogomphidae, Juracorduliidae, Juralibellulidae) (Nel & Paicheler 1994; Jarzembowski & Nel 1996; Bechly 1996, 1998; Fleck & Nel 2003; Huang & Nel 2007). Fleck et al. (2001) consider the Aeschnidiidae as very basal Cavilabiata. This group seems to have greatly diversified during the Early Cretaceous and 'replaced' the more ancient Mesozoic lineages (Isophlebioptera, Tarsophlebiidae, etc.). Ware et al. (2008) proposed estimated

divergence dates for the 'libelluloid' dragonflies based on molecular data. A comparison of the fossil data with their results is of interest (see below).

The exact affinities of the Mesozoic family Araripelibellulidae Bechly, 1996 remain difficult to establish. Thus every new fossil that contributes information is welcome. Nel & Paicheler (1994) described the 'corduliid' *Araripelibellula martinsnetoi* based on a single female specimen from the Crato Formation (north-east Brazil, Upper Aptian–Lower Albian in age) (Martill et al. 2007). The first male specimen of the same species is described herein and its phylogenetic implications are considered. The first representative of this genus in the English Lower Cretaceous is also described. A new specimen attributable to *Cretaneophya strevensi* Jarzembowski & Nel, 1996 gives more precise data on this enigmatic genus originally based on rather fragmentary wings. A new genus and species of Araripelibellulidae is also described from the Lower Cretaceous of China. Hitherto the only Mesozoic fossils attributed to the chlorogomphid lineage were the Lower Cretaceous Araripechlorogomphidae Bechly & Ueda, 2002; we describe two new fossils attributable to the new family Mesochlorogomphidae within Chlorogomphida from the Barremian (Lower Cretaceous) of England and Spain.

Acronyms of depositories

BMNH	Natural History Museum, London, UK
IEI	Institut d'Estudis Ilerdencs Museum, Lleida, Spain
MNEMG	Maidstone Museum and Bentlif Art Gallery, Maidstone, Kent, UK
MNHN	Muséum national d'Histoire naturelle, Paris, France

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2. Systematic palaeontology

The classification of fossil dragonflies is mainly based on wing venation as larval and adult body characters are generally not available. Fleck (2004), Fleck et al. (2008) and Pilgrim & von Dohlen (2008) demonstrated that the wing venation can be homoplasious in the Libellulidae, leading to erroneous attributions. Thus the present attributions of the new fossils are strictly dependent on the set of characters we use and the absence of a different set of characters that might contradict them.

The nomenclature of dragonfly wing venation used in this paper is based on the interpretations of Riek & Kukalová-Peck (1984), as amended by Nel et al. (1993) and Bechly (1996). For practical reasons, the higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 1998) and Bechly & Ueda (2002), although some characters and interpretations based on personal observation and unpublished data of one of us (G. F.) are not entirely compatible with this system for the clades Carinitibiata and Brachystigmata.

Order Odonata Fabricius, 1793
Clade Cavilabiata Bechly, 1996
Clade Paneurypalpida Bechly, 1996
Family Araripelibellulidae Bechly, 1996

Included genera: *Mesocordulia* Ren & Guo, 1996 (Lower Cretaceous, PR China); *Rencordulia* n. gen. (Lower Cretaceous, PR China); *Sopholibellula* Zhang et al., 2006 (Lower Cretaceous, PR China); *Araripelibellula* Nel & Paicheler, 1994 (Lower Cretaceous, Brazil, UK); *Cratocordulia* Bechly, 1998 (Lower Cretaceous, Brazil); *Cretaneophya* Jarzembowski & Nel, 1996 (Lower Cretaceous, UK); *Condalia* Whalley & Jarzembowski, 1985 (Lower Cretaceous, Spain).

Genus *Araripelibellula* Nel & Paicheler, 1994

Typus generis: *Araripelibellula martinsnetoi* Nel & Paicheler, 1994.

Further species: *Araripelibellula britannica* n. sp.

Araripelibellula martinsnetoi Nel & Paicheler, 1994
Figs. 1–4

Holotypus: Specimen MNHN-LP-R.54376 (female), Paris.

Locus typicus: Araripe Basin, N. E. Brazil.

Stratum typicum: Lower Cretaceous, Upper Aptian–Lower Albian, Crato Formation (Maisey 1990; De Miranda Lopes Neuman 1999; Martill et al. 1993, 2005).

Other material: Specimen B39, coll. ms-fossil (Bechly 1998, fig. 13) (complete female); new male specimen, BMNH II.1 (London), purchased by Santos P. in Fortaleza (Ceará) but from Santana do Cariri in origin. Other specimens have been mentioned by Bechly (2007: 217–218).

Description of BMNH II.1. – The new male specimen is an impression of the body with the four wings in connection, the right wings being nearly complete and the left wings apically broken.

Forewing (Fig. 1) 17.4 mm long, width opposite nodus 4.9 mm, distance from base to arculus 2.4 mm, from base to nodus 8.6 mm; from nodus to pterostigma 5.2 mm; from nodus to wing apex 8.8 mm (reconstructed length); nodus nearly midway between base and apex of wing; pterostigma short, strong and covering one cell, about 1.5 mm long, about 0.6 mm wide; pterostigmal brace distinctly oblique, rather well aligned with basal side of pterostigma; four antenodal crossveins, Ax1 and Ax2 barely stronger than the two not aligned secondaries; three postnodal crossveins; proximal postnodal crossvein in-

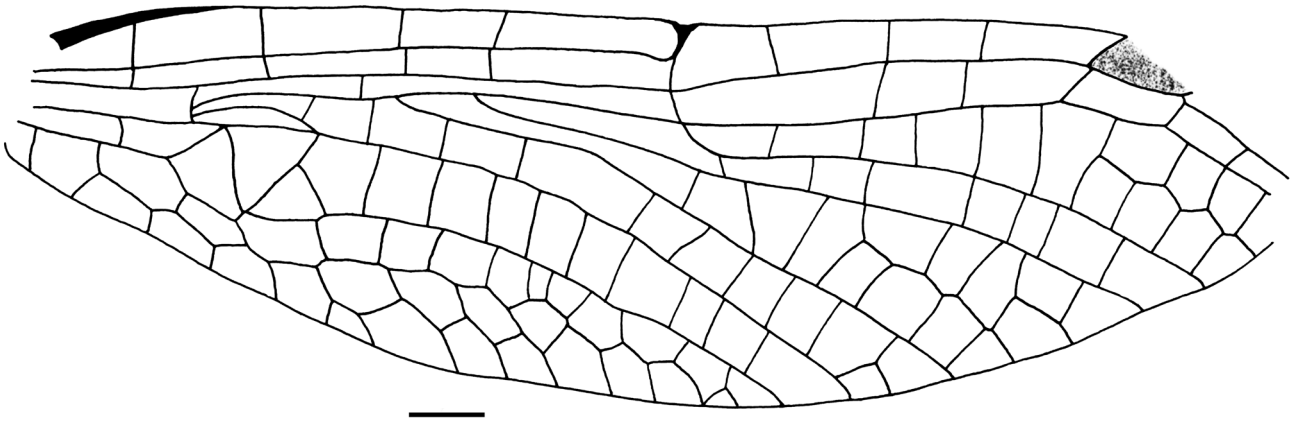

Fig. 1. *Araripelibellula martinsnetoi* NEL & PAICHELER, 1994, BMNH II.1, male, forewing; Upper Aptian–Lower Albian, NE Brazil. – Scale: 1 mm.

complete; arculus between Ax1 and Ax2 in a rather proximal position, 0.9 mm distal of first antenodal crossvein and 0.5 mm basal of discoidal triangle; MA and RP clearly separated at their base in arculus, 0.1 mm apart; free isosceles discoidal triangle, with anterior side straight; anterior side 1.2 mm long, proximal side 1.2 mm, distal side 1.3 mm; hypertriangle and median space free, MA arcuate at base; submedian space crossed by CuP; submedian and subdiscoidal spaces clearly separated by a strong oblique vein PsA; subdiscoidal space unicellular, 1.2 mm long, 0.9 mm wide; anal area not very broad, with two rows of cells; CuA not very long, with four short posterior branches and reaching posterior wing margin 1.5 mm basal of nodus; only two rows of cells in cubito-anal area, 1.2 mm wide; postdiscoidal area narrow, 0.9 mm wide, not distinctly widened near posterior wing margin, with only one row of cells; no Mspl; MA and RP3/4 more or less parallel and directed obliquely to posterior wing margin; only one antesubnodal crossvein; no Bq crossvein and no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; no distinct Rspl, only two rows of cells in distal part of area between RP3/4 and IR2; base of RP2 opposite subnodus; oblique crossvein 'O' 0.7 mm distal of subnodus; area between IR2 and RP2 slightly widened distally, these veins diverging near posterior wing margin; area between RP2 and RP1 narrow, with only two rows of cells at most and no definite vein IR1, only a zigzagged vein between these two rows of cells; no sigmoidal crossvein in proximal part of area between RP2 and RP1.

Hind wing (Figs. 2–4) about 16.5 mm long, 6.3 mm wide; width opposite nodus 5.9 mm; distance from base to arculus 1.5 mm, from base to nodus 5.7 mm, from nodus to pterostigma 6.5 mm, from nodus to apex about 10.8 mm (reconstructed length); nodus in a proximal position between base and apex; pterostigma 1.3 mm long, about 0.6 mm wide, short, covering less than one cell; pterostigmal brace distinctly oblique, aligned with basal side of pterostigma; three antenodal crossveins, all of the same strength; four postnodal crossveins with the two proximal incomplete; arculus in a very proximal position, opposite first antenodal crossvein and nearly opposite discoidal triangle; MA and RP clearly separated at their bases in arculus, 0.1 mm apart; free isosceles discoidal triangle, with anterior side slightly arched; length of anterior side 1.2 mm, of proximal side 0.9 mm, of distal side 1.1 mm; hypertriangle and median space free; MA strongly arcuate at base; submedian space crossed by CuP, no defined subdiscoidal space nor oblique vein PsA; anal area wide, with three rows of cells between AA and posterior wing margin; AA with two perpendicular branches directed towards posterior wing margin, proximal one enclosing a distinct two-celled anal triangle, 1.8 mm long and 0.9 mm wide; a weak anal angle at posterior end of anal triangle; distal branch of AA provides the basal side for a narrow, two-cells long anal loop, 2.6 mm long, 1.0 mm wide; anal loop with no midrib (Cuspl) but posteriorly closed by AA and CuAb; CuAa zigzagged, not very long, without distinct posterior branch, and reaching posterior wing margin 0.7 mm basal of nodus; only two or three rows of cells in cubito-anal area, 2.6 mm wide; postdiscoidal area narrow, 0.6 mm wide, distinctly broader near posterior wing margin, with only one row of cells in proximal part and four rows of cells along posterior wing margin; Mspl rudimentary; MA and RP3/4 parallel and obliquely reaching posterior wing margin; no Bq crossvein; only one antesubnodal crossvein in space between RA and RP, basal of base of RP3/4; only two crossveins in proximal part of area between RP3/4 and IR2, basal of nodus; no distinct vein Rspl; base of RP2 opposite subnodus; oblique crossvein 'O' 1.0 mm distal of subnodus; area between IR2 and RP2

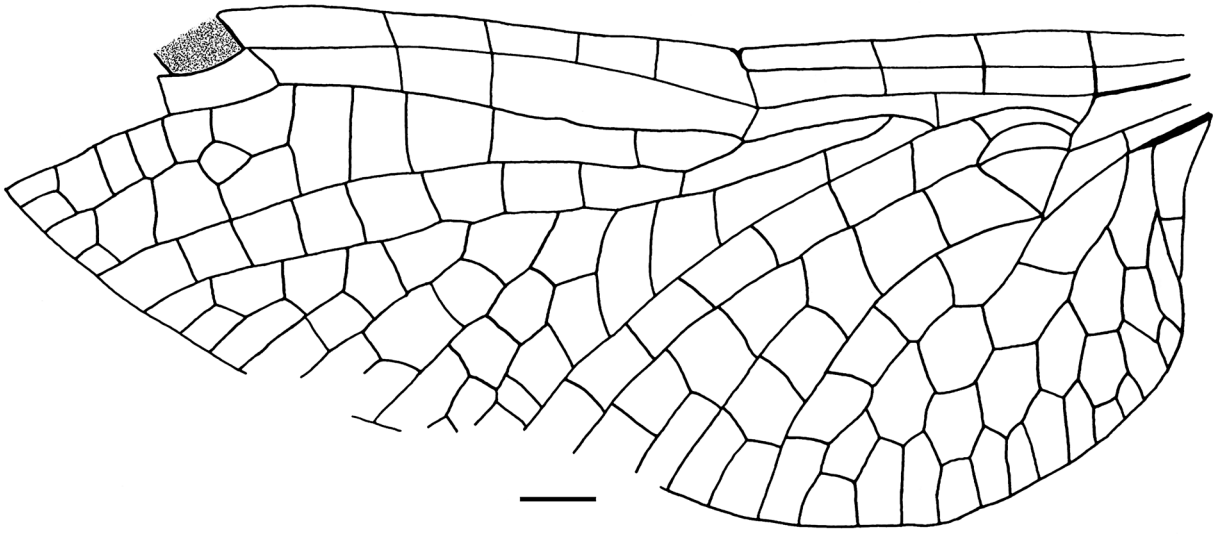

Fig. 2. *Araripelibellula martinsnetoi* Nel & Paicheler, 1994, BMNH II.1, male, hind wing; Upper Aptian–Lower Albian, NE Brazil. – Scale: 1 mm.

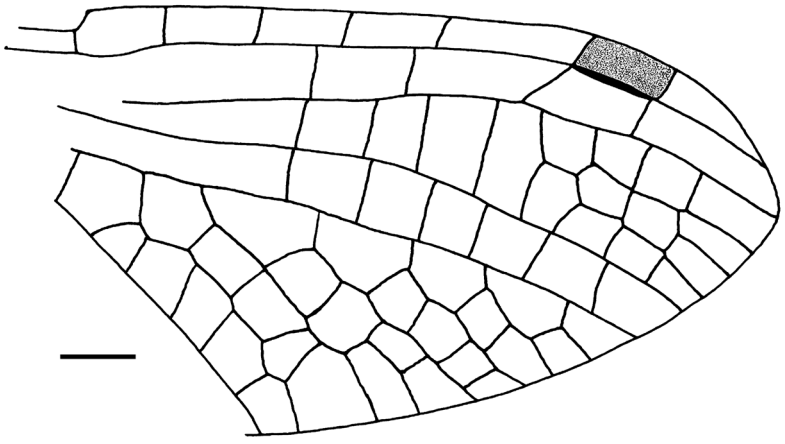

Fig. 3. *Araripelibellula martinsnetoi* Nel & Paicheler, 1994, BMNH II.1, male, hind wing apex; Upper Aptian–Lower Albian, NE Brazil. – Scale: 1 mm.

slightly widened distally; IR2 and RP2 directed obliquely to posterior wing margin; area between RP2 and RP1 narrow, with only two rows of cells and no definite IR1, only a zigzagged vein between them; no sigmoidal crossvein in proximal part of area between RP2 and RP1.

Colour pattern: whole forewing and distal part of hind wing (beyond nodus) fuscous; hind wing base hyaline, except for darkly pigmented anterior part (beyond supratriangle) and posterior edge.

Discussion. – The differences in the wing venation of the specimens MNHN-LP-R.54376 and BMNH II.1 are very few, namely the presence in the hind wing of BMNH II.1 of only two or three rows of cells in the anal area, of an anal triangle and an anal angle. R.54376, in contrast, has no anal angle, no anal triangle and a broader anal area, with four or five rows of cells between AA and the posterior wing margin. These differences are clearly of sexual origin, R.54376 being a female and BMNH II.1 a male. Other possible differences are due to problems of preservation for some crossveins, viz. a crossvein in the area between RA and RP, basal of base of RP3/4 visible in BMNH II.1 and apparently lacking in R.54376. Thus, these two specimens very likely belong to the same species. In the absence of any evidence to the contrary, we consider that they represent the male and the female of *Araripelibellula martinsnetoi*.

Bechly (1998) described another araripelibelluline genus *Cratocordulia* from the Crato Formation. BMNH II.1

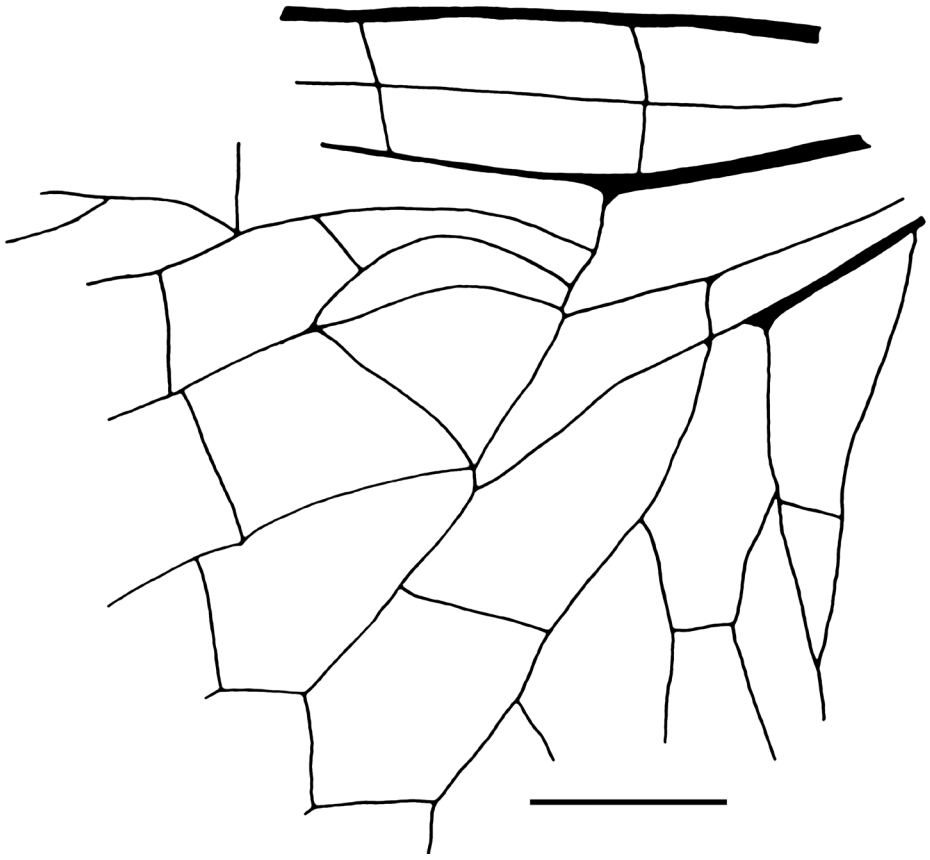

Fig. 4. *Araripelibellula martinsnetoi* NEL & PAICHELER, 1994, BMNH II.1, male, details of hind wing base; Upper Aptian–Lower Albian, NE Brazil. – Scale: 1 mm.

can be attributed to *Araripelibellula* rather than to this genus on the basis of the following characters: a) forewing Ax2 not basal of discoidal triangle, b) sectors of arculus well separated at base, c) anal loop two-celled and relatively short, d) MA and IR2 straight, and e) same number of postnodal and postsubnodal crossveins as in *Araripelibellula*.

The new male fossil confirms the fact that *Araripelibellula* has a small two-celled anal triangle, which was hitherto unknown.

Araripelibellula britannica n. sp.
Figs. 5–9

Holotypus: Specimen MNEMG 2008.24 [SCB/ODON 7], Maidstone, coll. R. A. CORAM (male hind wing).

Derivatio nominis: Named after the classical Latin name Britannia for Britain.

Stratum typicum: Soft Cockle beds (probably Bed DB66 of CLEMENTS 1993), Lulworth Formation, Purbeck Limestone Group; Lower Berriasian (ALLEN & WIMBLEDON 1991).

Locus typicus: Durlston Bay, Swanage, Dorset, UK (National Grid Reference SZ 035 780).

Further putative specimens: MNEMG 2008.25 [DB175/ODON 23] coll. R. A. CORAM, from Bed DB175 of CLEMENTS 1993, Corbula beds, Durlston Formation, Purbeck Limestone Group, Upper Berriasian, Durlston Bay, Swanage, Dorset, UK (ALLEN & WIMBLEDON 1991); Zt 9865 4683, British Geological Survey (bases of forewings), 'Lower Purbeck', precise horizon unknown, locality unknown, but probably also from Durlston Bay.

Description. – Holotype (Figs. 5–6). An impression of a nearly complete hind wing, with only the apical part missing. Wing about 22.0 mm long, 8.8 mm wide, width opposite nodus, 8.4 mm; distance from base to arculus, 2.6 mm, from base to nodus 8.6 mm, from nodus to pterostigma 9.8 mm, from nodus to wing apex about 13.5 mm; nodus in a proximal position; length and width of pterostigma unknown, although it was probably short; pterostigmal brace distinctly oblique; three antenodal crossveins, with distal antenodal crossvein complete and nearly as strong as the two primaries; seven postnodal crossveins, with two proximal postnodals incomplete and other postnodals not well aligned with corresponding

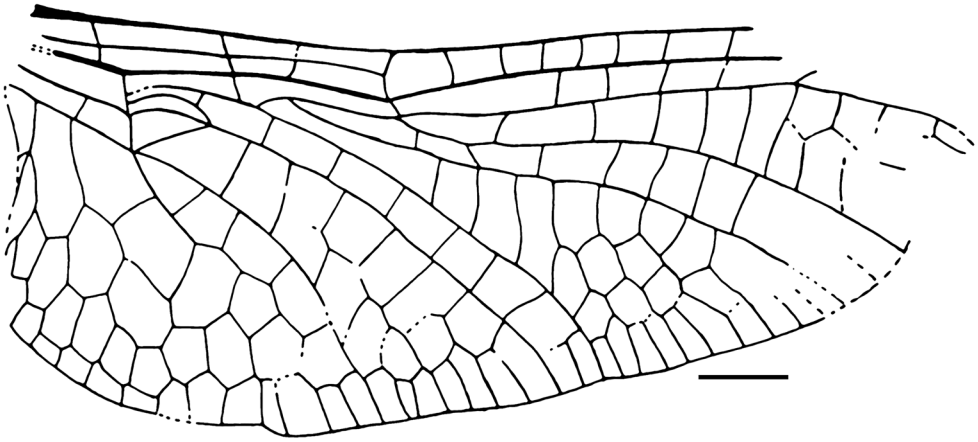

Fig. 5. *Araripelibellula britannica* n. sp., holotype MNEMG 2008.24, male, hind wing (diagenetic distortion of the wing corrected in drawing); Lower Berriasian, Dorset, UK. – Scale: 2 mm.

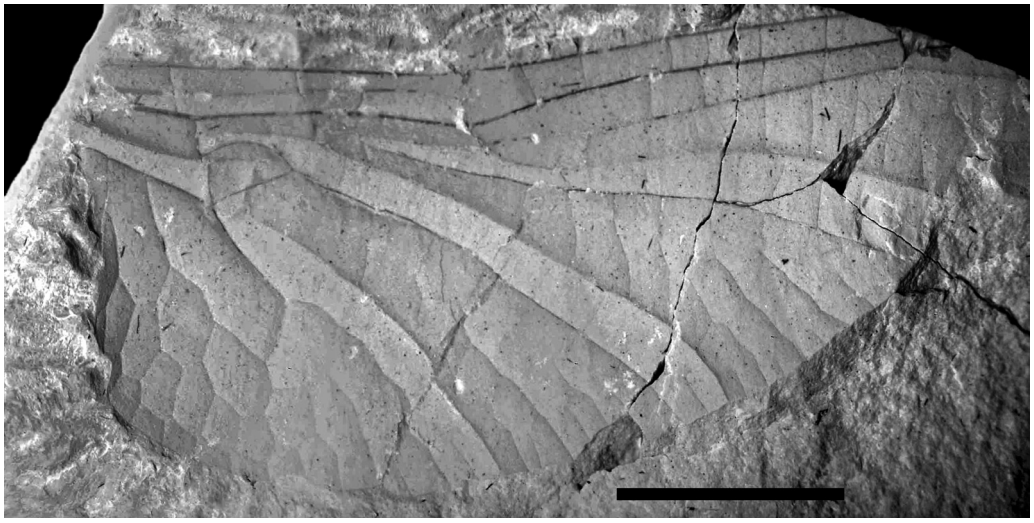

Fig. 6. *Araripelibellula britannica* n. sp., holotype MNEMG 2008.24, male, hind wing; Lower Berriasian, Dorset, UK. – Scale: 5 mm.

postsubnodal crossveins between RA and RP1; arculus in a rather proximal position, 0.5 mm distal of Ax1 and nearly aligned with discoidal triangle; MA and RP clearly separated at their bases in arculus, 0.3 mm apart; discoidal triangle free of crossveins, with anterior side slightly arched, anterior side 1.7 mm long, proximal side 0.8 mm long, distal side 1.8 mm long; hypertriangle and median space free; MA strongly arcuate at base; submedian space crossed by CuP without any defined subdiscoidal space nor oblique vein PsA; anal area wide, with three rows of cells between AA and posterior wing margin; AA with two posterior branches directed towards posterior wing margin, a distinct two-celled anal triangle, 2.2 mm long and 0.7 mm wide; an anal angle probably present at posterior end of anal triangle; distal branch of AA provides basal side for a narrow anal loop two-cells long, 4.6 mm long, 1.5 mm wide; anal loop without midrib (Cuspl), but closed posteriorly by AA and CuAb; CuA zigzagged, not very long, with no distinct posterior branches and reaching posterior wing margin 1.5 mm basal of nodus; only three rows of cells in cubito-anal area, 4.0 mm wide; postdiscoidal area narrow, 1.4 mm wide distal of triangle, distinctly broader near posterior wing margin, with only one row of cells in its proximal part and seven rows of cells along posterior wing margin; a rudimentary Mspl; MA and RP3/4 parallel and obliquely reaching posterior wing margin; apparently one Bq crossvein; no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; no distinct Rspl; base of RP2 opposite subnodus; oblique crossvein 'O', delimiting distal part of bridge

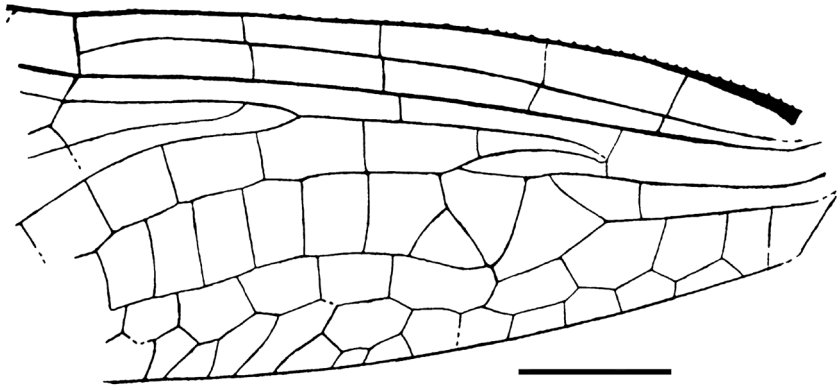

Fig. 7. *Araripelibellula britannica* (?) n. sp., MNEMG 2008.25, forewing; Upper Berriasian, Dorset, UK. – Scale: 2 mm.

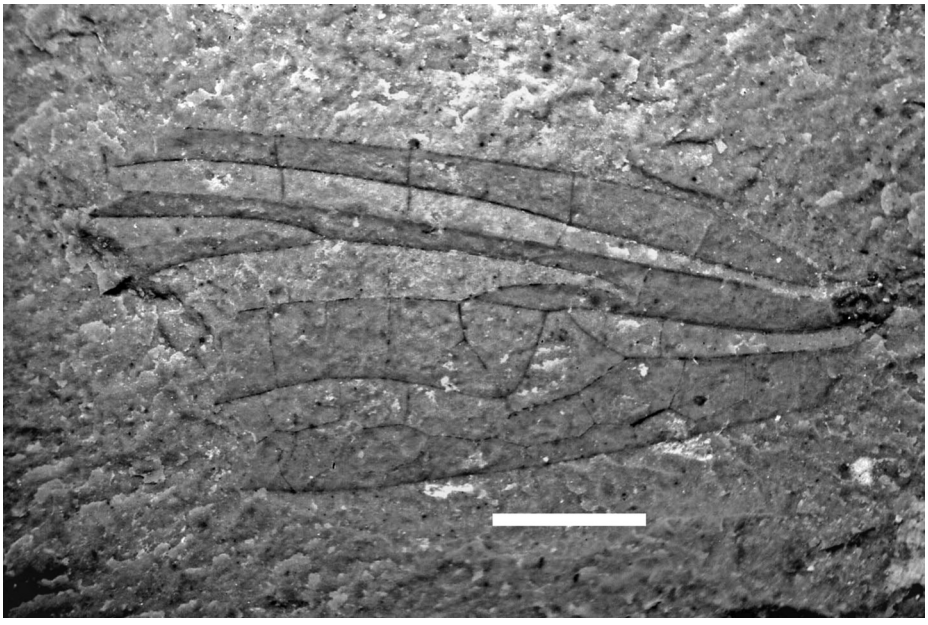

Fig. 8. *Araripelibellula britannica* (?) n. sp., MNEMG 2008.25, forewing; Upper Berriasian, Dorset, UK. – Scale: 2 mm.

space, 1.6 mm, two cells distal of subnodus, with a narrowing of area between IR2 and RP2 at its level; area between IR2 and RP2 slightly broadened distally; IR2 and RP2 directed obliquely to posterior wing margin; area between RP2 and RP1 narrow, with only two rows of cells and no definite IR1, only a zigzagged vein between them; an oblique crossvein in proximal part of area between RP2 and RP1.

Specimen MNEMG 2008.25 (Figs. 7–8). Basal half of a forewing; total length unknown; width opposite nodus 4.8 mm; distance from base to arculus 2.9 mm, from base to nodus 10.0 mm, from nodus to pterostigma and to apex unknown; length and width of pterostigma unknown; four antenodal crossveins, with distal one complete; primary antenodal crossveins slightly stronger than the two secondaries; arculus in a rather proximal position, 0.5 mm distal of Ax1 and 1.1 mm basal of discoidal triangle; MA and RP clearly separated at their base in arculus, 0.2 mm apart; discoidal triangle free, grossly quadrangular with anterior side shortly angled, distal side slightly angled, anterior side 1.1 mm long, proximal side 1.2 mm, distal side 1.3 mm; hypertriangle and median space free, basal part of MA arcuate; submedian space crossed by CuP; submedian and subdiscoidal spaces clearly separated by a strong oblique PsA; subdiscoidal space unicellular, 1.6 mm long, 1.1 mm wide; anal area not very wide, with two rows

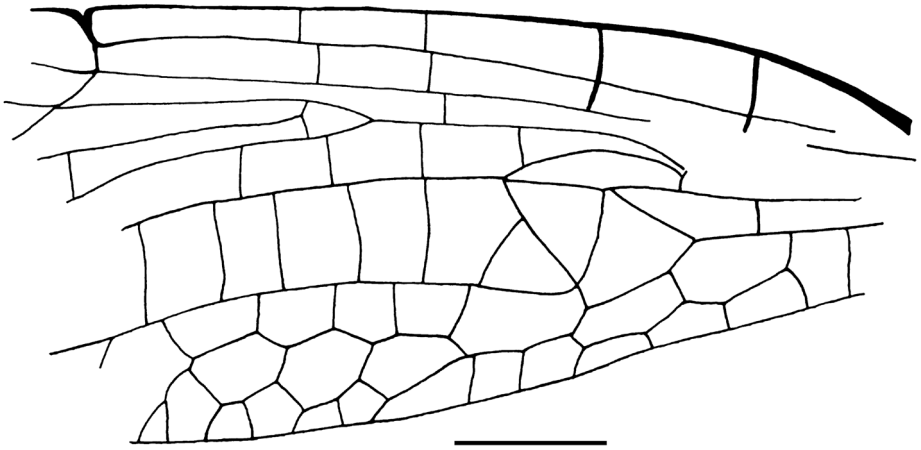

Fig. 9. *Araripelibellula britannica* (?) n. sp., Zt 9865, 4683, male forewing; Berriasian, Dorset, UK. – Scale: 2 mm.

of cells; CuA not very long, with four very short posterior branches and reaching posterior wing margin 1.2 mm basal of nodus; only 1–2 rows of cells in cubito-anal area, 1.0 mm wide; postdiscoidal area narrow, 1.1 mm wide, probably not distinctly widened near posterior wing margin, with only one row of cells in preserved part; probably no Mspl; MA and RP3/4 more or less parallel; no Bq crossvein and no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; base of RP2 opposite subnodus.

Specimen Zt 9865, 4683 (Fig. 9). Basal half of a forewing, very similar to MNEMG 2008.25 [DB175/ODON 23]. Main differences are as follows: width opposite nodus 6.0 mm; distance from base to nodus 11.3 mm; discoidal triangle free isosceles instead of quadrangular, anterior side straight, 1.3 mm long, proximal side straight, 1.3 mm long, distal side 1.7 mm long; two rows of cells in cubito-anal area, 1.4 mm wide, slightly broader than that of MNEMG 2008.25 [DB175/ODON 23]. We consider that these differences correspond to intraspecific variations.

Discussion. – Nel & Paicheler (1994) considered that *Araripelibellula* was related to the Lower Cretaceous genus *Eocordulia* Pritykina, 1986 (type genus of the Eocorduliidae Bechly, 1996) on the basis of the short, midrib-less anal loop and MA and RP3/4 separated basally (Pritykina 1986). However, these characters are symplesiomorphies of these taxa within the Corduliidae.

Bechly (1996, 1998) considered that the Eocorduliidae are the sister group of the Paneurypalpida Bechly, 1996 (= Araripelibellulidae + Eurypalpida Bechly, 1996) within the Eurypalpidiformia Bechly, 1996.

This last clade is supported by the synapomorphy 'pterostigma very shortened, only 1–2 cells long', which is probably the case for *Araripelibellula britannica* n. sp. The Eocorduliidae are supported by the synapomorphies: a) pterostigmal brace vein reduced (convergent to Cordulegastrida, Hemeroscopidae, Chlorogomphida, Valdicordulioidea, and some Eurypalpida), b) distinct Rspl and Mspl present, closely parallel to IR2 and MA respectively (convergent to many Eurypalpida, Aeshnoptera, and Aeschnidiidae), and c) more than one row of cells in distal half of area between RP3/4 and MA. All these characters are absent in *A. britannica* n. sp.

The Paneurypalpida are supported as follows: male hind wings with anal triangle divided into only two cells or even unicellular; forewing subdiscoidal triangle widened with a curved or angled posterior margin; pseudo-anal vein PsA and subdiscoidal triangle of hind wings more reduced than in groundplan of Cavilabiata (strong tendency towards complete reduction of the basal side PsA of the hind wing subdiscoidal triangle; convergent to Araripelibellulinae); subdiscoidal vein (basal part of CuA that is aligned with the distal side MAb of the discoidal triangle) reduced in hind wings; hind wing CuA (= AA+CuA sensu Fleck & Nel 2003 and Fleck et al. 2003) further shortened with only one distinct dichotomic branching into CuAa and CuAb (= (AA+CuA)a and (AA+CuA)b sensu Fleck et al. 2003; Fleck & Nel 2003); RP3/4 and MA secondarily not undulating, at least in hind wing; antenodal crossveins more or less aligned, at least hind wings with more than two aligned and bracket-like antenodal crossveins; basal part of postsubnodal area free of crossveins ('libellulid gap'), reversed in a few Libellulidae. All the characters that concern the hind wing are present in the holotype of *A. britannica* n. sp., and those that concern the forewing are present in the two forewings that we attribute to the same species.

A. britannica n. sp. has nearly all the synapomorphies of the Araripelibellulidae: Araripelibellulinae: a) no secondary antenodal crossveins between Ax1 and Ax2, and only two or three secondary antenodal crossveins distal of Ax2, b) all antenodal crossveins strictly aligned in the

hindwing (but the two primaries Ax1 and Ax2 are still stronger than the secondaries), c) only one or two antesubnodal crossveins, d) anterior side of hind wing hypertriangle strongly curved, and posterior side at least slightly curved, too, e) area between RP2 and IR2 very narrow near oblique vein 'O' (apomorphy), but more distally distinctly widened (plesiomorphy?), f) anal loop very elongate and narrow with only a single row of 2–4 cells (reduction), and g) PsA suppressed in hind wing (convergent to many crown-group Eurypalpida).

Furthermore, the two forewings tentatively attributed to *A. britannica* n. sp. have the further character 'postdiscoidal area very narrow in forewing (distal part even narrower than basal part), with only a single row of cells in basal half'. Then only the character 'forewing with only about four postnodal crossveins' would remain unknown in *A. britannica* n. sp. Thus we attribute all these fossil wings to the Araripelibellulinae.

Affinities of *A. britannica* n. sp. (type hind wing) with *Cratocordulia* are excluded on the basis of the following characters: a) sectors of arculus well separated at base, b) anal loop two-celled and relatively short, and c) MA and IR2 straight (Bechly 1998). The only character that is shared with *Cratocordulia borschukewitzi* Bechly, 1998 is the greater number of postnodal and postsubnodal crossveins than in *A. martinsnetoi*. Also, Ax2 is not basal of discoidal triangle in the fossil forewings we attribute to *A. britannica* n. sp.

It differs from *Cretaneophya* in that the sectors of the arculus are well separated at base (Jarzembowski & Nel 1996). Furthermore, the male hind wing of *Cretaneophya* differs from that of *A. britannica* n. sp. in its wider anal area with three, rather than two, rows of cells between the anal loop and the posterior margin.

Comparison with *Condalia woottoni* Whalley & Jarzembowski, 1985 is more difficult because this taxon is based on a single forewing (La Pedrera de Meià quarry, Spain, Barremian in age). Nevertheless, MA and RP3/4 are distally sigmoidal in *Condalia*, instead of being straight as in *A. britannica* n. sp. and *A. martinsnetoi*, which is a character currently present in both the forewing and hind wing of libelluloid dragonflies.

The differences between *A. britannica* n. sp. (based on the holotype hind wing) and *A. martinsnetoi* (based on the female holotype and the new male specimen) are few: a) three antenodal crossveins instead of 3–4 in *A. martinsnetoi*; b) seven postnodal crossveins instead of 3–4 in *A. martinsnetoi*; c) in the males, three rows of crossveins between anal loop and posterior wing margin instead of two (female specimens of *A. martinsnetoi*, like most of the females of "Corduliidae", have a broader anal area with four rows of cells between anal loop and posterior wing margin); d) an arculus more distant from Ax1 than in *A. martinsnetoi*; this character is rather variable as the arculus is opposite Ax1 in the male specimen of *A. martinsnetoi* and slightly separated from Ax1 in the known females; e) postdiscoidal area slightly broader along posterior wing margin than in *A. martinsnetoi*; f) hind wing longer than that of *A. martinsnetoi* (about 23 mm instead of 16.5 mm long). These differences cannot, however, justify a generic separation between the two taxa.

The attribution of the two forewings MNEMG 2008.25 [DB175/ODON 23] and Zt 9865, 4683 to *A. britannica* n. sp. is rather tentative. Nearly all the visible characters of these forewings are identical to those of *A. martinsnetoi*, except for the stronger primary antenodal crossveins. But they are also very similar to those of the forewing of *Condalia woottoni*. Nevertheless, the forewing of *C. woottoni* is 7.5 mm wide at the discoidal cell level, instead of 4.1–4.8 mm in MNEMG 2008.25 [DB175/ODON 23] and Zt 9865, 4683, which is more compatible with *A. martinsnetoi* (3.8 mm in specimen BMNH II.1).

Thus, in the absence of any evidence to the contrary, we consider that the two forewings MNEMG 2008.25 and Zt 9865, 4683 probably belong to the new species *A. britannica* n. sp.

Genus *Cretaneophya* Jarzembowski & Nel, 1996

Typus generis: *Cretaneophya strevensi* Jarzembowski & Nel, 1996

Cretaneophya strevensi Jarzembowski & Nel, 1996
Fig. 10

New material: Specimen MNEMG 2008.26 [AY 94 148, 211], Maidstone, coll. Tony Mitchell.

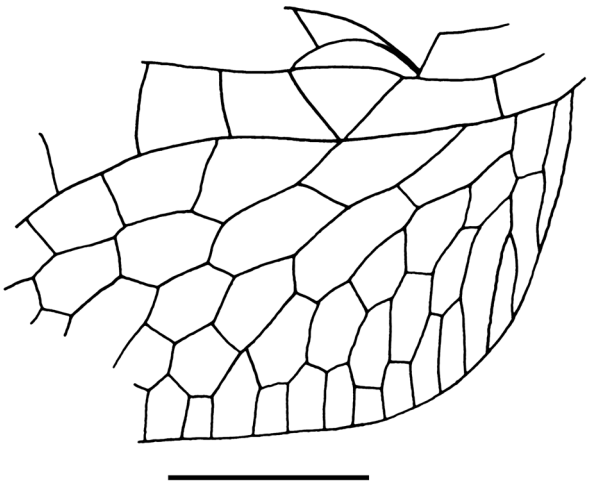

Fig. 10. *Cretaneophya strevensi* Jarzembowski & Nel, 1996, MNEMG 2008.26, postero-basal part of hind wing; Lower Barremian, Surrey, UK. – Scale: 2 mm.

Age and Horizon: Lower Cretaceous, Early Barremian, Upper Weald Clay (Allen & Wimbledon 1991).

Locality: Auclaye Brickworks, Surrey, UK (National Grid Reference TQ 169 389).

Description. – This new specimen is from the same locality and stratum as the holotype. It is the impression of the postero-basal part of a hind wing, very similar to those of the type series. Nevertheless, it has some different venational features: a) RP and MA are basally very close but are not fused as in other specimens, and b) the arculus is not precisely aligned with the proximal side of the discoidal triangle. All other characters are identical to those of the type series. Thus this new specimen provides further information on the variation in venation within this species.

Genus *Rencordulia* n. gen.

Typus generis: *Rencordulia sinica* n. sp.

Derivatio nominis: Named after Dr. Ren Dong, Chinese palaeoentomologist, and the genus *Cordulia*.

Diagnosis. – Wing characters only. Fore- and hind wing: four or five postnodal crossveins, with the two or three most basal incomplete; discoidal triangles free and isosceles; two rows of cells in postdiscoidal areas just distal of triangles; area between IR2 and RP2 distally narrowed, IR1 distinct; pterostigma covering one cell or nearly so, pterostigmal brace distinct, aligned with basal side of pterostigma; area between RP3/4 and IR2 broad; hypertriangle with anterior margin curved but posterior margin straight or nearly so. Forewing: six antenodal crossveins, last one apparently incomplete; RP3/4 and MA sigmoidal, with postdiscoidal area distally not broadened; PsA strong, subdiscoidal space crossed; CuAa with rudimentary branches. Hind wing: three antenodal crossveins, all well aligned; six-celled elongated anal loop, with poorly defined pseudo-midrib not reaching anal vein; vein PsA absent.

Discussion. – *Rencordulia* n. gen. has all the synapomorphies of the Paneurypalpida as listed above. But it lacks several synapomorphies of the Eurypalpida Bechly, 1996, sister group of the Araripelibellulidae, viz. a) sectors of arculus distinctly more approximate, generally diverging from one point or even shortly fused basally, b) arculus distinctly more straight in both pairs of wings, and c) pterostigmal brace vein shifted distally beneath the pterostigma, or reduced.

Rencordulia n. gen. has the synapomorphies of the Araripelibellulidae, viz. a) no secondary antenodal crossveins between Ax1 and Ax2, and only two or three secondary antenodal crossveins distal of Ax2, b) all antenodal crossveins aligned or nearly so (but Ax1 and Ax2 still stronger than secondaries), c) only one or two antesubnodal crossveins, d) forewing with only about four postnodal crossveins, e) anterior side of hind wing hypertriangle at least rather strongly curved, and posterior side at least slightly curved, too, f) forewing postdiscoidal area very narrow (distal part even narrower than basal part), and g) anal loop very elongate.

The anal loop of *Rencordulia* n. gen. is more elongate and broader than in the known Araripelibellulidae, but it has fewer cells than most of the Eurypalpida. The area between RP2 and IR2 is not distinctly widened distally, unlike in the Araripelibellulidae, but this character may be related to the more numerous cells in the distal halves of its wings than in the other Araripelibellulidae.

Araripelibellula, *Cratocordulia*, *Cretaneophya*, and *Condalia* have far fewer cells than *Rencordulia* n. gen., especially in the postdiscoidal area. Only *Mesocordulia* Ren & Guo, 1996 and *Sopholibellula* Zhang et al., 2006 from the same level as *Rencordulia* n. gen. have approximatively the same density of cells in their wings. *Rencordulia* n. gen. differs from *Mesocordulia* in its six-celled anal loop, with pseudo-midrib not reaching the anal vein; and vein PsA completely absent in the hind wing (Ren & Guo 1996, figs. 8, 10). *Sopholibellula* differs from *Rencordulia* n. gen. in the vein PsA completely absent and the incomplete secondary antenodal crossveins in the forewing (Zhang et al 2006). These differences justify a generic separation and an attribution of *Rencordulia* n. gen. to the Araripelibellulinae.

Rencordulia sinica n. sp.
Figs. 11–13

Holotypus: Specimen MNHN-LP-R.63890, Paris.

Derivatio nominis: Named after the Latin name for China.

Stratum typicum: Yixian Formation, Lower Cretaceous (Zhang et al. 2006, 2008).

Locus typicus: Jianshangou, Beipiao City, Liaoning Province, PR China.

Diagnosis. – Same as genus (monotypic).

Description. – A complete dragonfly in lateral aspect (Fig. 11). Forewing (Fig. 12) 24.6 mm long, width opposite nodus 6.7 mm, distance from base to arculus 3.1 mm, from base to nodus 12.7 mm; from nodus to pterostigma 6.9 mm; from nodus to wing apex 11.7 mm; nodus nearly midway between base and apex of wing; pterostigma short, strong and covering one cell, about 2.0 mm long, 0.8 mm wide and with proximal and distal sides rather strongly divergent; pterostigmal brace distinctly oblique, aligned with basal side of pterostigma; six antenodal crossveins, Ax1 and Ax2 stronger than the secondaries, 2.3 mm apart, secondaries of first row not exactly aligned with those of second row; four postnodal crossveins; distal antenodal crossvein incomplete; two proximal postnodal crossveins incomplete; arculus in a proximal position, only 0.5 mm distal of first antenodal crossvein and 0.9 mm basal of discoidal triangle; MA and

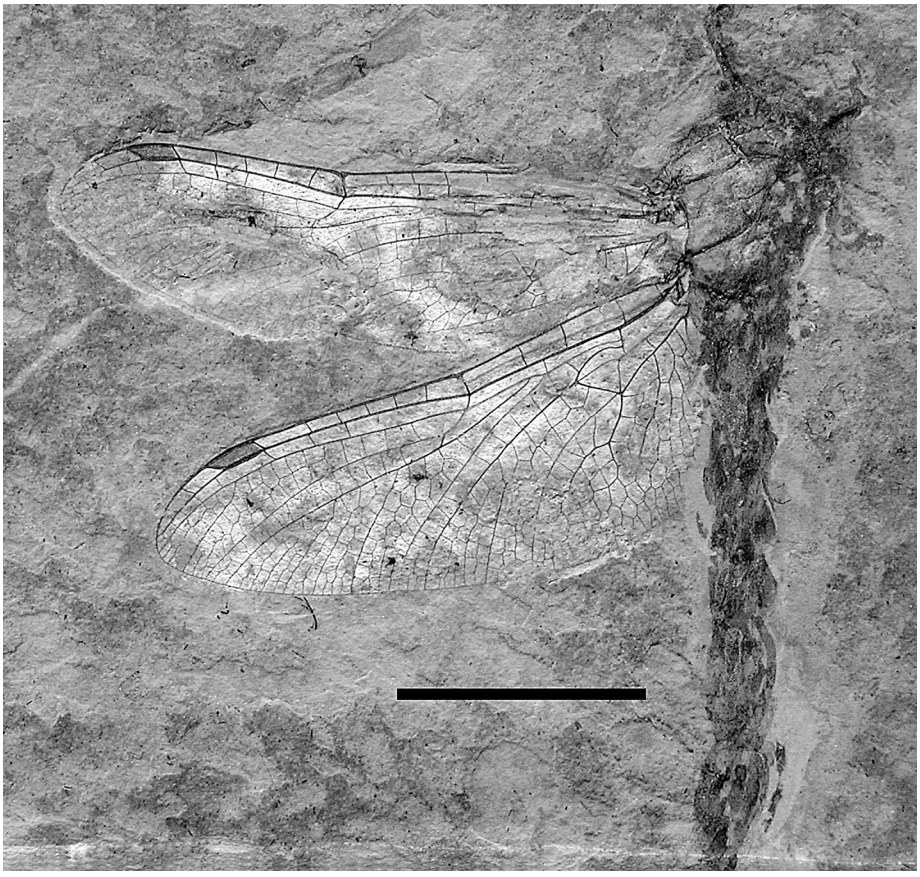

Fig. 11. *Rencordulia sinica* n. gen., n. sp., holotype, MNHN-LP-R.63890, general habitus; Yixian Formation, Lower Cretaceous, Liaoning, PR China. – Scale: 10 mm.

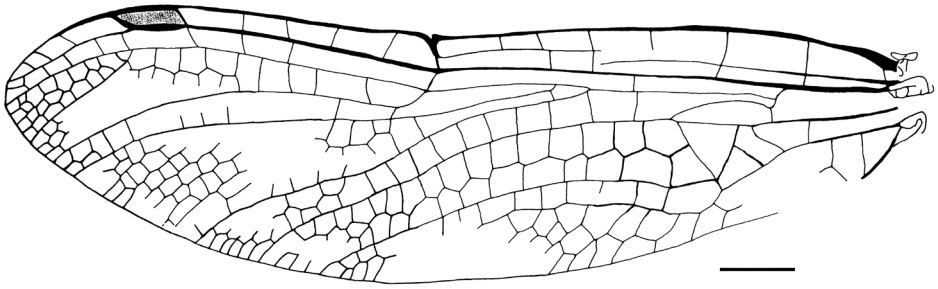

Fig. 12. *Rencordulia sinica* n. gen., n. sp., holotype, MNHN-LP-R.63890, forewing; Yixian Formation, Lower Cretaceous, Liaoning, PR China. – Scale: 2 mm.

RP clearly separated at their base in arculus, 0.3 mm apart; free isosceles discoidal triangle, with anterior side straight; anterior side 1.6 mm long, proximal side 1.6 mm, distal side 1.8 mm; hypertriangle and median space free, MA arcuate at base; submedian space crossed by CuP; submedian and subdiscoidal spaces clearly separated by a strong oblique vein PsA; subdiscoidal space two-celled (?), 1.9 mm long, 1.3 mm wide; anal area not very broad, with two rows of cells; CuA not very long, with 4–5 posterior branches and reaching posterior wing margin below nodus; three or four rows of cells in cubito-anal area, 1.8 mm wide; postdiscoidal area narrow, 1.6 mm wide, with two rows of cells distal of triangle, not widened near posterior wing margin, with four rows of small cells; no Mspl; MA and RP3/4 undulate, more or less parallel and directed obliquely to posterior wing margin, with area

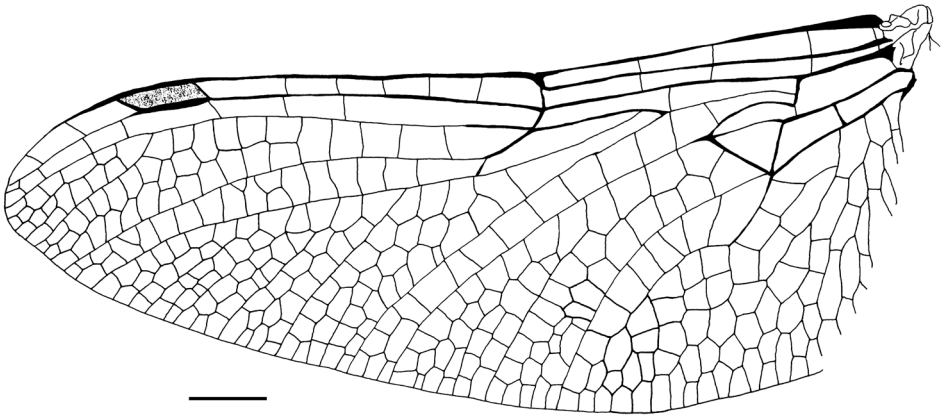

Fig. 13. *Rencordulia sinica* n. gen., n. sp., holotype, MNHN-LP-R.63890, hind wing; Yixian Formation, Lower Cretaceous, Liaoning, PR China. – Scale: 2 mm.

between them broadened near posterior wing margin; no Bq crossvein and no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; only one antesubnodal crossvein in space between RA and RP, basal of base of RP3/4; no distinct Rspl, 8–9 rows of cells in distal part of area between RP3/4 and IR2; base of RP2 opposite subnodus; oblique crossvein 'O' 1.0 mm, one cell distal of subnodus; area between IR2 and RP2 slightly narrowed distally, these veins converging near posterior wing margin; area between RP2 and RP1 narrow, with seven rows of cells at most and a short but distinct vein IR1, no sigmoidal crossvein in proximal part of area between RP2 and RP1.

Hind wing (Fig. 13) 26.9 mm long, 9.1 mm wide; width opposite nodus 8.6 mm; distance from base to arculus 2.5 mm, from base to nodus 9.2 mm, from nodus to pterostigma 8.6 mm, from nodus to apex 14.2 mm; nodus in a proximal position between base and apex; pterostigma 2.3 mm long, 0.8 mm wide, short, covering less than one cell and with proximal and distal sides divergent; pterostigmal brace distinctly oblique, aligned with basal side of pterostigma; three antenodal crossveins, all of the same strength; five postnodal crossveins with the three proximal incomplete; arculus in a proximal position, just distal of first antenodal crossvein and nearly opposite discoidal triangle; MA and RP clearly separated at their bases in arculus, 0.3 mm apart; free isosceles discoidal triangle, with anterior side nearly straight; length of anterior side 1.8 mm, of proximal side 1.4 mm, of distal side 1.8 mm; hypertriangle and median space free; MA strongly arcuate at base; submedian space crossed by CuP, no defined subdiscoidal space nor oblique vein PsA; anal area wide, with six rows of cells between AA and posterior wing margin; AA with three perpendicular branches directed towards posterior wing margin, proximal one enclosing a distinct two-celled anal triangle, 2.0 mm long and 0.3 mm wide; anal angle not preserved; distal branch of AA provides the basal side for a long and narrow six-cells anal loop, 4.7 mm long, 1.4 mm wide, with a ill defined zigzagged midrib; subdiscoidal vein (basal part of CuA that is aligned with the distal side MAb of the discoidal triangle) reduced; gaff of CuA elongated and slightly curved; CuAa distally zigzagged, not very long, with no well-defined posterior branches, and reaching posterior wing margin 1.8 mm basal of nodus; five rows of cells in cubito-anal area, 4.0 mm wide; postdiscoidal area narrow, 1.5 mm wide distal of triangle, distinctly broader near posterior wing margin, with two rows of cells in proximal part and 11 rows of cells along posterior wing margin; Mspl rudimentary; MA and RP3/4 parallel and obliquely reaching posterior wing margin; no Bq crossvein; no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; only one antesubnodal crossvein in space between RA and RP, basal of base of RP3/4; no distinct vein Rspl; base of RP2 opposite subnodus; oblique crossvein 'O' 1.4 mm distal of subnodus; area between IR2 and RP2 slightly narrowed distally; IR2 and RP2 directed obliquely to posterior wing margin; median area between RP2 and RP1 with 3–4 rows of cells; a short IR1, no sigmoidal crossvein in proximal part of area between RP2 and RP1.

Clade Chlorogomphida Bechly, 1996
Family Mesochlorogomphidae n. fam.

Typus familiae: *Mesochlorogomphus* n. gen.
Other genus: *Hispanochlorogomphus* n. gen.

Diagnosis. – Only hind wing characters known. Anal loop long and broad, divided into numerous cells but without midrib and toe; CuAa and CuAb not strictly aligned; CuAb directed towards postero-basal wing margin; CuAa with two or three branches; subdiscoidal triangle distinct-

ly slanted towards hind margin, basally dilated, but distally abruptly narrowed; PsA strong; discoidal triangle transversely crossed; hypertriangle, median and submedian spaces free of crossveins (except Cup in the submedian space); cubital cell (between CuP-crossing and PsA) free; one or two secondary antenodals between Ax1 and Ax2; secondary antenodal crossveins of first and second rows not aligned; postnodal crossveins and postsubnodal crossveins not aligned; pterostigma covering 1–3 cells; basal and distal sides of pterostigma not parallel; no pterostigmal brace; no Mspl; IR1 short; anal and cubito-anal areas broad at base; MA and RP distinctly separated in arculus; only two or three crossveins in area between RA and RP basal of base of RP3/4 or IR2 ('cordulegastrid gap'); oblique vein 'O' one cell distal of subnodus.

Discussion. – The Mesochlorogomphidae n. fam. represents the potential sister group of the clade Chlorogomphoidea + Araripechlorogomphidae within the Chlorogomphida. Both *Mesochlorogomphus* n. gen. and *Hispanochlorogomphus* n. gen. have plesiomorphic characters relative to the clade (Chlorogomphoidea + Araripechlorogomphidae). One potential synapomorphy of the Mesochlorogomphidae n. fam. could be the hind wing discoidal cell being divided into two small cells by a transverse crossvein, an unusual character in the Cavilabiata.

Remark. – The characters of the wing venation are possibly much prone to homoplasy than previously assumed (see above). Within the Cavilabiata, the Chlorogomphoidea present some unique plesiomorphies not related to wing venation, like a larval mandible with a moveable molar crest, or a larval gizzard with remnant of rasp-like dentition (Fleck, pers. obs.).

Thus the members of the Chlorogomphida are possible sister-groups of the remaining Cavilabiata, or sister-group of the (Neopetaliidae + Cordulegastridae) (Fleck & Nel, unpublished). However, other non-wingvenational morphological characters conflict with such a position, and the posterior probability for closer relationship of chlorogomphids and libelluloids was 99 % in the Bayesian molecular study by Ware et al. (2007). Further studies are necessary to solve this problem.

Genus *Mesochlorogomphus* n. gen.

Typus generis: *Mesochlorogomphus crabbi* n. sp.

Derivatio nominis: Named after the Mesozoic and *Chlorogomphus*.

Diagnosis. – Only hind wing characters known. Subdiscoidal space crossed; two secondary crossveins between the two primaries; only two branches of CuAa (main branch plus distal vein secondarily branched on CuAa); two rows of cells between MP and CuAa just distal of discoidal triangle. For differences from *Hispanochlorogomphus* n. gen. see there.

Discussion. – The presence of a 'cordulegastrid gap', the elongate gaff (= basal CuA before its branching) of the hind wing, and RP3/4 and MA slightly undulating are apomorphies of the Cavilabiata. The absence of a fork of IR2 basal of the lestine oblique vein 'O', the very distinct PsA, and the very large anal loop exclude affinities with the Cordulegastrida (after Bechly 1996, 1998). The pterostigma not parallel sided (distal side more oblique than basal side) and rather stout, and the hind wing CuAa shortened, with few (0–6) posterior branches are apomorphies supporting this species' attribution to the Cristotibiata Bechly, 1998 (= Neopetaliidae and Brachystigmata Bechly, 1996). The short intercalary vein IR1 excludes affinities with the Neopetaliidae Tillyard & Fraser, 1940 (after Bechly 1996, 1998). The short pterostigma covering only 1–3 complete cells, the hind wing gaff strongly elongated and very straight, the area between MP and CuA basally widened with more than one row of cells, and the terminal branch of CuAa secondarily branched (on CuA) are apomorphies of the Brachystigmata. The large anal loop and the presence of two secondaries between Ax1 and Ax2 exclude affinities with the Nannogomphidae Bechly, 1996. The presence of less than five branches of CuAa supports the attribution to the nanogomphid sister group Eubrachystigmata Bechly, 1998. Within this clade, the character 'arculus not distinctly angled but more or less straight, with posterior part distinctly shorter than anterior part' is an apomorphy of the Paraneobrachystigmata Huang & Nel, 2007, the sister group of the Hemeroscopidae Pritykina, 1977. The character 'MP distinctly curved towards hind margin and thus somewhat shortened, ending basal of level of nodus' is then the synapomorphy of the Neobrachystigmata Bechly & Ueda, 2002, sister group of the Middle Jurassic family Juralibellulidae Huang & Nel, 2007.

Within the Neobrachystigmata, the character analysis is more problematic since there are similarities between the Chlorogomphida Bechly, 1996 ('chlorogomphid' lineage) and the Paneurypalpidomorpha Bechly & Ueda, 2002 ('libelluloid' lineage).

The potential synapomorphies with Chlorogomphida are: a) typical shape of subdiscoidal triangle in hind wing, i. e. distinctly slanted towards hind margin, basally dilated, but distally abruptly narrowed (although convergently present in the paneurypalpidomorphan family Araripephlebiidae Bechly, 1998); b) pterostigmal brace vein reduced (convergent with some Eurypalpida); and c) anal loop longitudinally elongated and broad (comprising at least 7–9 cells) and of characteristic pentagonal shape.

One apomorphy of the Paneurypalpidomorpha is not present in *Mesochlorogomphus* n. gen., supporting its exclusion from this clade, i. e. 'Ax1 and Ax2 relatively close together with not more than one secondary antenodal crossvein between them'. Also, *Mesochlorogomphus*

n. gen. cannot belong in the most basal family of this clade, Juracorduliidae Bechly & Ueda, 2002 (based on *Juracordulia* Bechly, 1998) because its anal loop is of different shape, its postdiscoidal area is broad, and its RP3/4 and MA are undulating. It cannot belong to its sister group Eurypalpidomorpha Bechly & Ueda, 2002 (= [(Valdicorduliidae Bechly, 1996 + Araripephlebiidae Bechly, 1998) + (Eocorduliidae Bechly, 1996 + Paneurypalpida)]) because the elongated gaff in the hind wing is straight, not sigmoidally curved (but this character is reversed in Synthemistidae Tillyard, 1911, which have no hind wing PsA and sectors of arculus stalked unlike in *Mesochlorogomphus* n. gen.). Nevertheless, *Mesochlorogomphus* n. gen. shares with the Eurypalpidomorpha the apomorphy 'CuAa with only one or two posterior branches'. However, this character is also present in chlorogomphids, viz. *Araripechlorogomphus* Bechly & Ueda, 2002 and *Chlorogomphus* Selys, 1854. Thus we consider *Mesochlorogomphus* n. gen. as a chlorogomphidan. The hind wing discoidal triangle of Araripechlorogomphidae Bechly & Ueda, 2002 is unicellular, unlike *Mesochlorogomphus* n. gen. Also, the shape of the anal loop of *Mesochlorogomphus* n. gen. differs from that of *Araripechlorogomphus* and Chlorogomphoidea in that CuAb is directed towards the postero-basal wing margin in the former (plesiomorphy), and directed towards the wing base in the latter taxa (apomorphy).

Mesochlorogomphus n. gen. lacks the main apomorphies of the Chlorogomphoidea Needham, 1903, viz. a) sectors of arculus are approximate, b) basal accessory antenodal crossveins present in subcostal space between Ax0 and Ax1, c) hind wing discoidal triangle divided into 2–6 cells, d) presence of crossveins immediately basal of subnodus ('cordulegastrid gap' reduced), e) median space

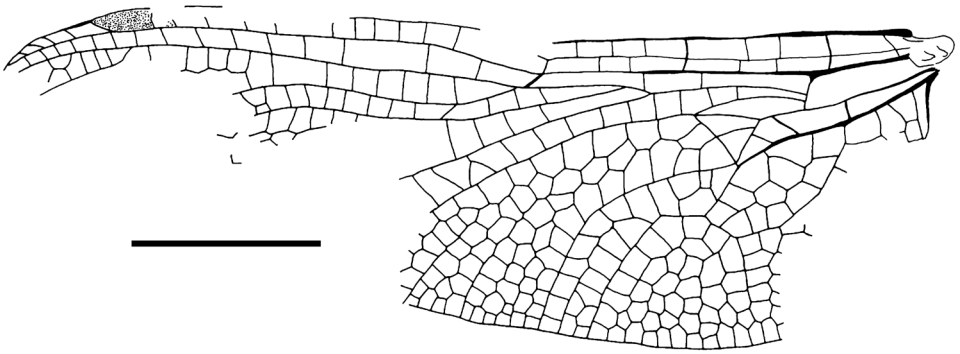

Fig. 14. *Mesochlorogomphus crabbi* n. gen., n. sp., holotype, MNEMG 2008.27, hind wing; Barremian, Surrey, UK. – Scale: 5 mm.

Fig. 15. *Mesochlorogomphus crabbi* n. gen., n. sp., holotype, MNEMG 2008.27, hind wing; Barremian, Surrey, UK (Photo: P. Crabb). – Scale: 5 mm.

crossed, and f) cubital cell (between CuP-crossing and PsA) divided by accessory cubito-anal crossveins. Thus *Mesochlorogomphus* n. gen. cannot be considered as a chlorogomphoidean.

Mesochlorogomphus crabbi n. sp.
Figs. 14–15

Holotypus: Specimen MNEMG 2008.27, Maidstone.

Derivatio nominis: Named after Mr. P. Crabb, fossil finder and photographer.

Stratum typicum: Lower Cretaceous, Barremian, Upper Weald Clay (Allen & Wimbledon 1991).

Locus typicus: Smokejacks Brickworks, Surrey, UK (National Grid Reference TQ 113 373).

Diagnosis. – Same as genus (monotypic).

Description. – Impression of a rather complete hind wing, with basal part of anal area and distal part of posterior margin missing; wing 26.6 mm long, 8.4 mm wide; distance from base to nodus 11.0 mm, from nodus to wing apex 15.6 mm, from nodus to pterostigma 10.4 mm; nodus in a basal position; pterostigma 2.4 mm long, 0.6 mm wide, covering two and a half cells; pterostigmal brace cannot be distinguished from other crossveins between RA and RP1; 11–12 postnodal crossveins, not aligned with crossveins between RA and RP1; seven antenodal crossveins, secondary crossveins of first row not aligned with corresponding crossveins of second row; two primary antenodal crossveins stronger than secondaries, with two secondaries between them; distance from wing base to Ax1 2.8 mm; from Ax1 to Ax2 4.0 mm; Ax2 nearly opposite distal angle of discoidal triangle and Ax1 0.6 mm basal of arculus; RP and MA distinctly separated at their bases in arculus; arculus not distinctly angled, with posterior part (crossvein) distinctly shorter than anterior part [RP and MA]; only two crossveins in area between RA and RP, basal of base of IR2 and none between base of IR2 and subnodus; two crossveins between RP and MA above discoidal hypertriangle; arculus basally recessed close to Ax1, 1.4 mm basal of discoidal triangle; hypertriangle and median space free of crossveins; submedian space crossed by CuP; PsA strong; subdiscoidal space two-celled, 1.8 mm long, 0.8 mm wide; isoceles two-celled discoidal triangle, with anterior side nearly straight, 1.8 mm long, proximal side 1.4 mm long, distal side 1.8 mm long; a very well defined anal loop, longer than broad, without midrib and toe, and divided into twelve cells, 4.6 mm long, 2.0 mm wide; basal part of CuA very long and nearly straight; CuAb directed towards wing base; CuAa strongly curved and without definite secondary branch, except for a ill defined zigzagged longitudinal secondary vein in distal part of area between CuAa and MP that can be interpreted as the terminal branch of CuA which should be secondarily branched on CuA; anal area very broad, with ten rows of cells between AA and posterior wing margin, six rows of cells between anal loop and posterior wing margin; cubito-anal area broad, with six rows of cells between CuAa and posterior wing margin; two rows of cells between CuA and MP just distal of discoidal triangle; MP distinctly curved towards hind margin and thus somewhat shortened, ending basal of level of nodus; three rows of cells in postdiscoidal area just distal of discoidal triangle, this area being distally greatly broadened; no Mspl; MA and RP3/4 weakly curved and gradually diverging distally; three 'Bq' crossveins in space between RP, IR2, RP2 and oblique crossvein 'O'; one crossvein in space between RP3/4 and IR2 basal of subnodus; oblique crossvein 'O' 1.9 mm and two cells distal of subnodus; RP2 nearly aligned with subnodus; Rspl only partly preserved, with one row of cells between it and IR2; IR2 and RP2 undulate and parallel in the preserved part; area between RP2 and RP1 broadened nearly midway between subnodus and pterostigma; a short but distinct IR1 beginning below distal half of pterostigma.

Genus *Hispanochlorogomphus* n. gen.

Typus generis: *Hispanochlorogomphus rossi* n. sp.

Derivatio nominis: Named after the genus *Chlorogomphus* and Hispania, Latin name for Spain.

Diagnosis. – The hind wing venation of *Hispanochlorogomphus* n. gen. is very similar to that of *Mesochlorogomphus* n. gen., differing from it only in few characters, such as: subdiscoidal space free, instead of divided by a crossvein; only one secondary crossvein between the two primary antenodals, instead of two; one branch of CuAa just distal of anal loop and basal of main branch of CuAa; one row of cells between MP and CuAa just distal of discoidal triangle, instead of two.

Hispanochlorogomphus rossi n. sp.
Figs. 16–17

Holotypus: Specimen LP-0096-G, IEI Museum in Lleida, Spain.

Derivatio nominis: Named after our colleague and friend Dr. Andrew Ross.

Stratum typicum: Lower Cretaceous, Barremian.

Locus typicus: La Pedrera de Meià, Sierra del Montsec, Lleida, Spain (Martínez-Delclòs & Ruíz de Loizaga 1993; Martínez-Delclòs & Peñalver-Molla 1999).

Diagnosis. – Same as genus (monotypic).

Description. – Impression of a nearly complete hind wing, with part of cubito-anal area and distal part of posterior margin missing. Wing 23.7 mm long, 8.7 mm wide; width at nodus level 8.3 mm; distance from base to nodus 9.5 mm, from nodus to wing apex 13.8 mm, from nodus to pterostigma 9.5 mm; nodus in a basal position; pterostigma

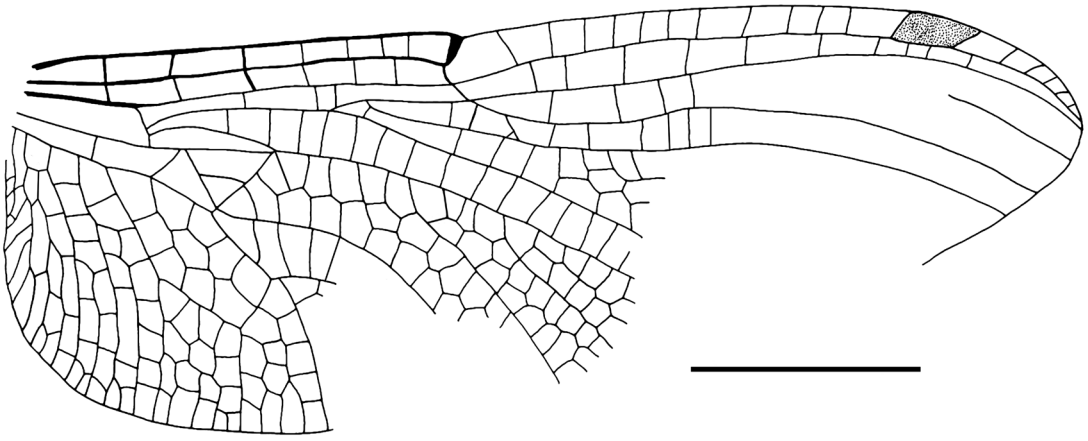

Fig. 16. *Hispanochlorogomphus rossi* n. gen., n. sp., holotype, LP-0096-G, hind wing; Barremian, Sierra del Montsec, Spain. – Scale: 5 mm.

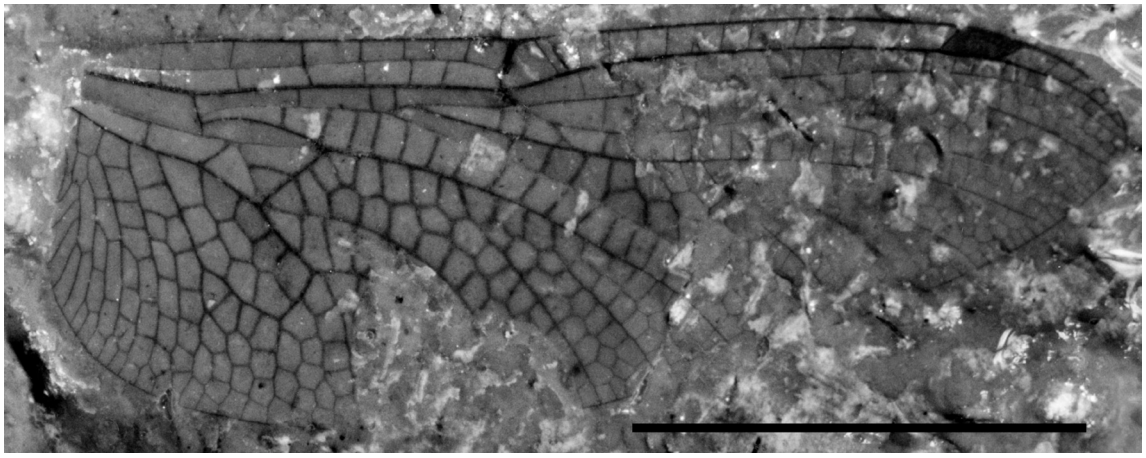

Fig. 17. *Hispanochlorogomphus rossi* n. gen., n. sp., holotype, LP-0096-G, hind wing; Barremian, Sierra del Montsec, Spain. – Scale: 10 mm.

1.8 mm long, 0.7 mm wide, covering two and a half cells; pterostigmal brace absent; about eleven postnodal crossveins, not aligned with postsubnodal crossveins, 'libellulid gap' reduced; seven antenodal crossveins (including primaries), the secondaries being not well aligned with corresponding crossveins between ScP and RA; Ax1 and Ax2 distinctly stronger than secondaries, with one secondary between them; distance from wing base to Ax1 1.6 mm, between Ax1 and Ax2 1.6 mm; Ax2 nearly opposite distal angle of discoidal triangle and Ax1 0.8 mm basal of arculus; RP and MA distinctly separated at their bases in arculus; three crossveins in area between RA and RP, basal of base of IR2 and none between base of IR2 and subnodus ('cordulegastrid gap'); two crossveins between RP and MA above hypertriangle; arculus basally recessed, close to Ax1, 0.7 mm basal of discoidal triangle; posterior part of arculus distinctly shorter than anterior part; hypertriangle and median space free; submedian space crossed by CuP; strong PsA separating subdiscoidal space and submedian space; subdiscoidal space unicellular triangle, 1.6 mm long, 0.8 mm wide; two-celled isosceles discoidal triangle, with anterior side nearly straight, 1.6 mm long, proximal side 1.2 mm long, distal side 2.0 mm long; anal loop very well defined, longer than broad, without midrib and toe, and divided into ten cells, 4.3 mm long, 1.6 mm wide; basal stem of CuA very long and nearly straight; CuAb directed towards postero-basally; CuAa strongly curved, with at least two secondary branches, possibly three (most distal one not preserved); anal area very broad, with eight rows of cells between AA and posterior wing margin, four rows of cells between anal loop and posterior wing margin; AA with five posterior branches, the most distal one being the basal side of the anal loop; anal margin rounded with no anal angle and no anal triangle (female?); cubito-anal area

broad, with five rows of cells between CuAa and posterior wing margin; one row of broad and narrow cells between CuA and MP just distal of discoidal triangle; MP distinctly curved towards hind margin and ending basal of level of nodus; two rows of cells in postdiscoidal area just distal of discoidal triangle but this area greatly broadens distally; no Mspl; MA and RP3/4 nearly straight and more or less parallel; two 'Bq' crossvein in space between RP, IR2, RP2 and oblique crossvein 'O'; one crossvein in space between RP3/4 and IR2 basal of subnodus; oblique crossvein 'O' 0.9 mm and one cell distal of subnodus; RP2 aligned with subnodus; basal part of a rudimentary vein Rspl apparently present, but the main part of this vein is missing; IR2 and RP2 weakly curved and parallel; area between RP2 and RP1 distally broadened, nearly midway between subnodus and pterostigma; a short but poorly preserved vein IR1, beginning opposite distal half of pterostigma.

Discussion. – The same characters as noted above for *Mesochlorogomphus* n. gen. support the attribution of *Hispanochlorogomphus* n. gen. to the Chlorogomphida.

4. Estimated divergence dates for 'libelluloid' dragonflies

The discovery of two new Araripelibellulidae in the Lower Cretaceous of the UK and China demonstrates that this family was probably very diverse and widespread. Also, the discovery of the new chlorogomphid family Mesochlorogomphidae in the Barremian (Lower Cretaceous) of the UK and Spain confirms the considerable diversity and morphological disparity of the late Mesozoic libelluloid dragonflies.

In their estimated divergence dates for the 'libelluloid' dragonflies based on molecular data, Ware et al. (2008) largely ignored the recent advances in palaeontology, except for the paper of Jarzembowski & Nel (1996). As an example, Ware et al. (2008) proposed the estimated divergence dates 87.6 Myr or 57.7 Myr for the Libellulidae, while the first known representative of this family is dated from the Turonian (circa 90 Myr), suggesting an older age for this clade (Fleck et al. 1999).

Ware et al. (2008) proposed an Early Jurassic age for the Chlorogomphida while their oldest fossil record is Early Cretaceous (Araripechlorogomphidae and Mesochlorogomphidae). These authors also assumed that the 'Libelluloidea' diverged 249 Myr ago, during the Triassic. But the oldest known libelluloid is Middle Jurassic and the oldest Anisoptera (Liassogomphidae) are Early Jurassic (Nel et al. 1993). The earliest representatives of the other modern anisopteran groups (Petalurida, Aeshnoptera, Gomphides) are also Middle to Late Jurassic, not Triassic. The only Triassic Epiproctophora (clade that comprises the former 'Anisozygoptera' plus the Anisoptera) belong to the clade Isophlebioptera, which have a rather basal position in the epiproctophoran phylogeny (Fleck et al. 2003). Furthermore, they are Late, not Early Triassic, in age. The oldest representatives of the more derived clades that are potential sister groups of the anisopteran lineage (Heterophlebiomorpha, Stenophlebioptera) are also Early Jurassic. Thus it is very unlikely that the 'Libelluloidea' originated during the Early (or Late) Triassic. The Cavilabiata probably appeared during the Early to Middle Jurassic and greatly diversified during the Early Cretaceous.

Ware et al. (2008) indicated that the evaluation of the various hypotheses that could explain the evolution of the dragonflies relies on realistic dating estimates. However they failed to do this as they neglected fossils. Accurate information on the age of the 'libelluloid' dragonflies clearly requires further research on fossils.

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Addresses of the authors:

Dr. Günther Fleck, Museu Integrado de Roraima, Av. Brigadeiro Eduardo Gomes, Parque Anauá, 69305-010 Boa Vista, Roraima, Brazil
E-mail: gfleck@uni-bonn.de

Dr. André Nel, UMR CNRS 5202, Entomologie, CP 50, Muséum national d'Histoire naturelle, 45 rue de Buffon, 75005, Paris, France
E-mail: anel@mnhn.fr

Dr. Günter Bechly, Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany
E-mail: bechly.smns@naturkundemuseum-bw.de

Dr. Xavier Delclòs, Departament d'Estratigrafia, Paleontologia i Geociències Marines, Facultat de Geologia, Universitat de Barcelona, 08071, Barcelona, Spain
E-mail: xdelclos@ub.edu

Dr. Edmund A. Jarzembowski, Maidstone Museum and Bentlif Art Gallery, St Faith's St, Maidstone, Kent ME14 1LH and SHES, University of Reading, UK
E-mail: edjarzembowski@maidstone.gov.uk

Robert A. Coram, 6 Battlemead, Swanage, Dorset, BH19 1PH, UK
E-mail: rob@britishfossils.co.uk

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