



HAL
open science

Phase contrast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae)

Malvina Lak, Gunther Fleck, Dany Azar, Michael-S. Engel Fls, Hani-F. Kaddumi, Didier Neraudeau, Paul Tafforeau, André Nel

► To cite this version:

Malvina Lak, Gunther Fleck, Dany Azar, Michael-S. Engel Fls, Hani-F. Kaddumi, et al.. Phase contrast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae). *Zoological Journal of the Linnean Society*, 2009, 156 (4), pp.913-923. 10.1111/j.1096-3642.2008.00497.x . insu-00425186

HAL Id: insu-00425186

<https://insu.hal.science/insu-00425186>

Submitted on 7 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NoDerivatives 4.0 International License

Phase contrast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae)

MALVINA LAK^{1,2}, GÜNTHER FLECK^{3,4*}, DANY AZAR⁵, MICHAEL S. ENGEL FLS⁶, HANI F. KADDUMI⁷, DIDIER NERAUDEAU¹, PAUL TAFFOREAU² and ANDRÉ NEL^{3*}

¹Université Rennes 1, CNRS UMR 6118, 263 avenue du Général Leclerc, 35042 Rennes cedex, France

²European Synchrotron Radiation Facility, BP 220, 6 rue Jules Horowitz, 38043 Grenoble cedex, France

³CNRS UMR 5202, Muséum National d'Histoire Naturelle, Entomologie, CP 50, 45 rue Buffon, F-75005 Paris, France

⁴Museu Integrado de Roraima, Av. Brigadeiro Eduardo Gomes, Parque Anauá, 69305-010 Boa Vista, Roraima, Brazil

⁵Lebanese University, Faculty of Sciences II, Department of Biology, Fanar – Matn – P. O. box 26110217, Lebanon

⁶Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66049-2811, USA

⁷Eternal River Museum of Natural History, P.O. Box 11395, Amman, Jordan

Received 7 May 2008; accepted for publication 30 June 2008

***Electrohemiphlebia barucheli* gen. et sp. nov.** and ***Jordanhemiphlebia electronica* gen. et sp. nov.**, two new genera and species are described, based on exceptional inclusions of hemiphlebiid damselflies in Cretaceous amber from France and Jordan. The type specimen of *E. barucheli* was studied using phase contrast X-ray synchrotron microtomography, giving exceptional images and detailed information. Its comparison with the recent *Hemiphlebia mirabilis* confirms the attribution of several Cretaceous damselflies to the Hemiphlebiidae, showing that this particular group was widespread in the Early Cretaceous and probably originated in the Late Jurassic or earlier. The ecological niches today occupied by the small coenagrionoid damselflies were occupied during the Triassic and Jurassic by Protozygoptera, hemiphlebiids during the Early Cretaceous, and modern taxa in the Cenozoic.

© 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 156, 913–923.
doi: 10.1111/j.1096-3642.2008.00497.x

ADDITIONAL KEYWORDS: early Cretaceous – faunistic changes – France – gen. nov. – Jordan – sp. nov..

INTRODUCTION

Although the insect order Odonata has a rich and varied fossil record, those species of the familiar suborder Zygoptera (i.e. the damselflies) are significantly more rare in Mesozoic deposits than the dragonflies and damsel-dragonflies (suborder Epiproctophora). To

date, only five genera from the Late Jurassic and about ten from the Cretaceous have been described (Bechly, 1998b; Jarzembowski *et al.*, 1998; Fleck *et al.*, 2001), and all as compressions with little or no relief. Fossil odonates in amber are quite rare and to date only recorded from the Tertiary. This lack of an ‘amber record’ is disheartening given the unique fidelity of preservation in amber and the wealth of systematic and palaeobiological information that can be ascertained from such inclusions.

*Corresponding authors. E-mail: gfleck@uni-bonn.de, anel@mnhn.fr

Herein we report the oldest damselflies in latest Albian amber from south-western France and Barremian amber from Jordan, the latter of contemporaneous age with the more extensive deposits of Lebanese amber (Brenner & Bickoff, 1992). The uniqueness of the present discoveries most probably does not correspond to a rarity of damselflies in the contemporaneous palaeoenvironments but rather to a taphonomic bias. Odonata are very rare in all types of amber, even in Dominican (about 20 specimens), Oise, France (three specimens), and Baltic amber (fewer than 50 specimens), where several thousands of other arthropod inclusions are trapped (Bechly, 1998a; May & Carle, 2005; Nel & Arillo, 2006). Indeed, the present discovery of a damselfly among fewer than 2000 biological inclusions in Jordanian amber corresponds to a potentially higher percentage than to those in Baltic amber (Kaddumi, 2005). Damselflies are actually rather common in lacustrine and fluvial outcrops of the same age.

The French specimen is preserved in a piece of opaque amber and was discovered and studied with phase contrast X-ray synchrotron imaging (Tafforeau *et al.*, 2006; Lak *et al.*, 2008). Its wings, head, legs, and thorax are preserved, but the abdomen is lacking. The Jordanian specimen is represented solely by the distal half and basal half of a hyaline wing, with dark brown pterostigma. Only two small fragments of the wing are not preserved, namely the section just distal to the nodus and the basalmost portion of the wing. The preserved structures of the wings of these fossils present a high degree of similarity to those of small damselflies from the Barremian sandstones of the English Weald Clay and the Lacustrine Crato Formation in Brazil, i.e. the hemiphlebiid genera *Parahemiphlebia* and *Cretarchistigma* (Bechly, 1998b; Jarzembowski *et al.*, 1998).

MATERIAL AND METHODS

The French specimen (ARC 372.1) is the second Odonata found in the Mid Cretaceous deposits from the Charentes region. The first one, a dragonfly, corresponds to a wing print in the Early Cenomanian clay from the Puy-Puy quarry (Nel *et al.*, 2008). The new specimen, from the latest-most Albian of the Archingeay-Les Nouillers quarry (Néraudeau *et al.*, 2002), was firstly detected (but not recognized) during a large survey of Charentes opaque amber using propagation phase contrast X-ray synchrotron microradiography, following the protocol described in Lak *et al.* (2008). It was then three-dimensionally imaged using phase contrast X-ray synchrotron microtomography. These two experiments were performed on the Beamline ID19 of the European

Synchrotron Radiation Facility (ESRF) at Grenoble, France. Details for the microradiographic survey protocol were given by Lak *et al.* (2008). The microtomographic scan was performed with an isotropic voxel size of 5.06 µm with a monochromatic beam at an energy of 30 keV and a propagation distance of 990 mm. As the size of the amber block was far larger than the tomographic field of view, we used local microtomography with 1500 projections on 180 degrees in continuous acquisition mode (Lak *et al.*, 2008). After tomographic reconstruction and eight-bits conversion, the volume was segmented in 3D using the software VGStudioMax 1.2.1 (Volume Graphics, Heidelberg, Germany), in order to virtually extract the specimen from the opaque amber.

In the descriptions, wing venation nomenclature follows that of Riek (1976) and Riek & Kukalová-Peck (1984), as amended by Nel *et al.* (1993), Bechly (1996), and Fleck & Nel (2003).

The following standard abbreviations are used: AA anal vein, AP anal posterior, Ax1 and Ax2 primary antenodal cross-veins, CuAa distal branch of cubitus anterior, CuAb proximal branch of cubitus anterior, IR2 intercalary radial vein, MAa distal branch of median anterior, MAb posterior branch of median anterior, MA median anterior, MP median posterior, N nodus, Pt pterostigma, RA radius anterior, RP radius posterior RP3/4 proximal branch of radius posterior.

SYSTEMATIC PALAEONTOLOGY

FAMILY HEMIPHLEBIIDAE TILLYARD, 1926

ELECTROHEMIPHLEBIA GEN. NOV.

Etymology: The genus-group name is a combination of the Greek term *electron* (meaning, 'amber') and *Hemiphlebia*, type genus of the family. The name is feminine.

Type species: *Electrohemiphlebia barucheli* sp. nov.

Diagnosis: Very small damselflies; head not very transverse; clypeofrontal sulcus deep; antefrons with two strong gibbosities separated by a median depression; strong sulcus between frons and vertex (i.e. the plate bearing the ocelli, limited anteriorly by the frons, laterally by the eyes and posteriorly by the occiput); posterior ocelli on a high gibbosity well separated from others and from the vertex and frontal part of frons by complete sulci set inside strong depressions; suture between vertex and occiput rather well pronounced; pterothoracic interpleural suture only present around metastigmal area; protibial comb absent; wings with short petiole;

arculus distinctly distal of Ax2; forewing discoidal cell basally opened, with RP + MA, basal part of MA, and MAb aligned or nearly so; angle between MAb and MP + CuA rather acute in forewing discoidal cell; hindwing discoidal cell basally closed; base of RP3/4 close to subnodus; base of IR2 opposite subnodus; subnodus vertical.

***ELECTROHEMIPHLEBIA BARUCHELI* GEN.**

ET SP. NOV. (FIGS 1–14, 20A, B)

Etymology: The specific epithet is a patronymic one, proposed by Paul Tafforeau, honouring José Baruchel, head of the imaging group of the ESRF, as without him, palaeontology would never had developed so importantly at the ESRF.

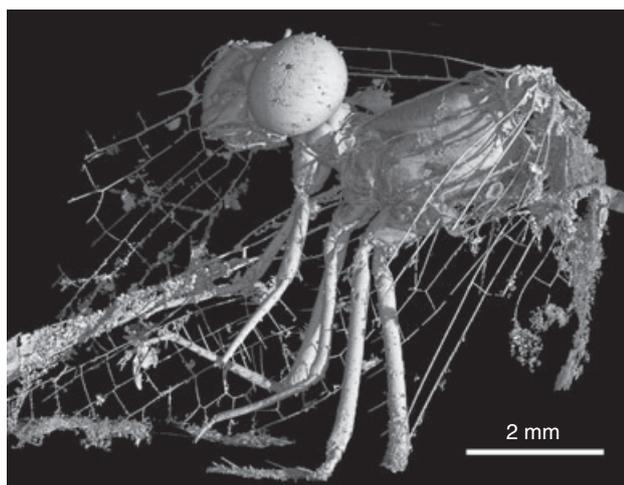


Figure 1. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, habitus left lateral view.

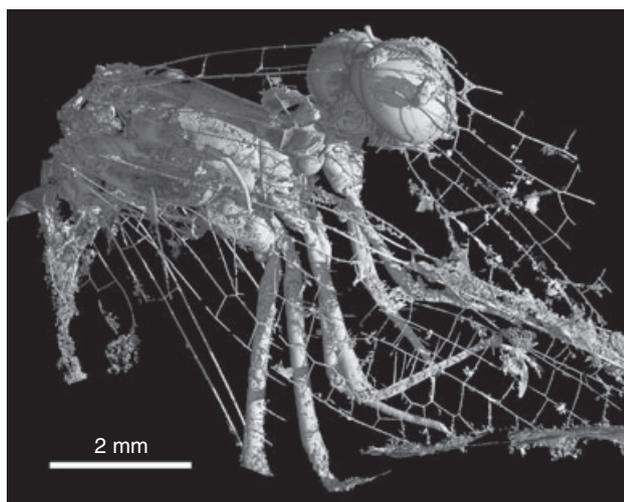


Figure 2. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, habitus right lateral view.

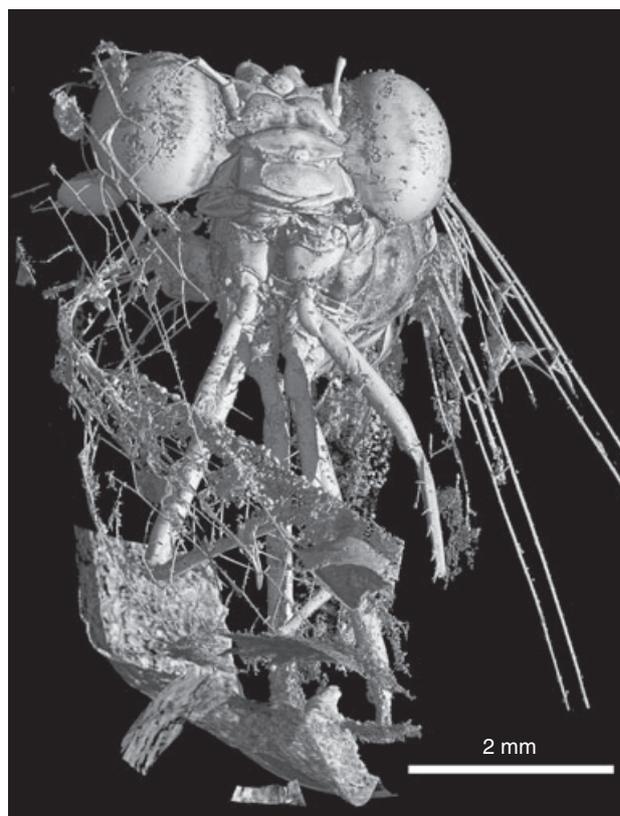


Figure 3. *Electrohemiphlebia barucheli* gen. nov., sp. nov., holotype ARC 372.1, habitus frontal view.

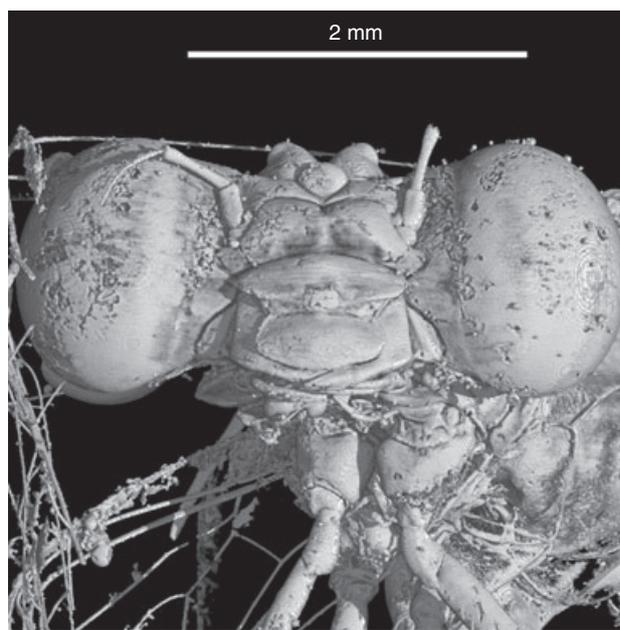


Figure 4. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, frontal view of head.

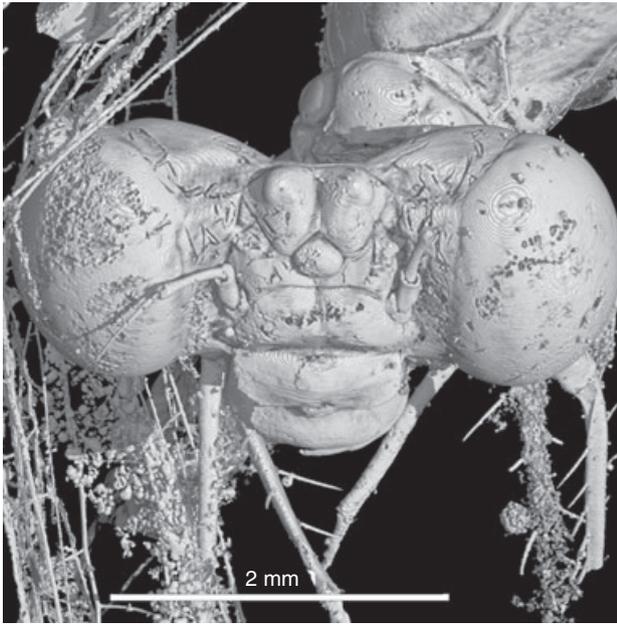


Figure 5. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, dorsal view of head.

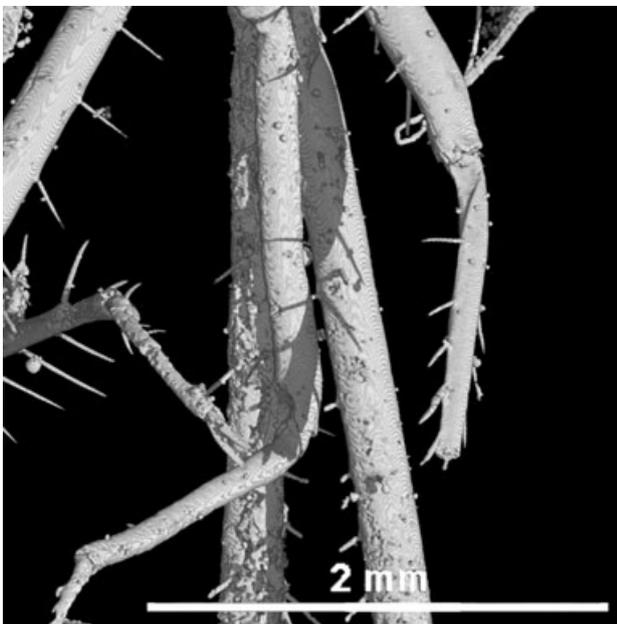


Figure 6. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, detail of fore legs (white arrow for tibia).

Material: Holotype specimen ARC 372.1, a complete thorax attached to head and to the basal parts of the four wings, deposited in the Department Histoire de la Terre, Muséum National d'Histoire Naturelle, Paris. All the tomographic data as well as a surface model of the specimen are available upon request

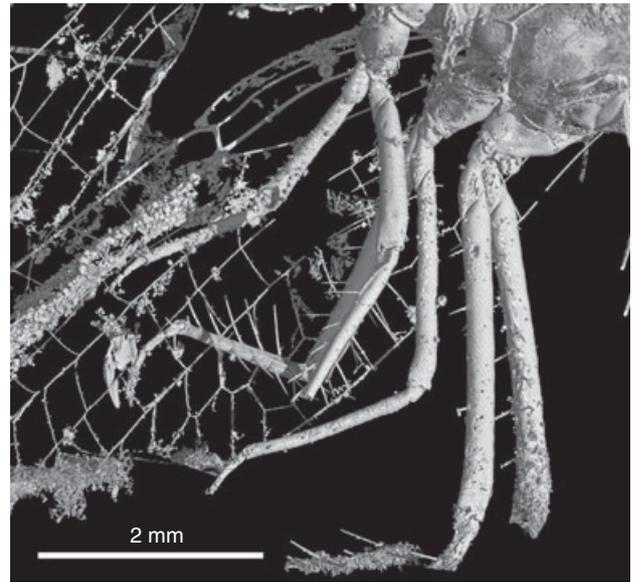


Figure 7. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, legs.

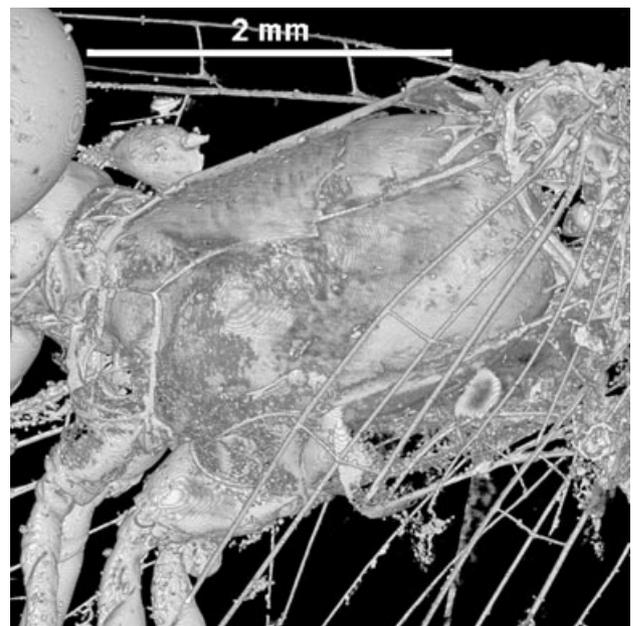


Figure 8. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, left view of thorax.

from the first author, and will be deposited in the public palaeontological database project of the ESRF when available. Reference 3D prints of the extracted specimens are deposited in the Muséum National d'Histoire Naturelle (Paris, France), in the Géosciences laboratory (Rennes, France), and at the ESRF (Grenoble, France).

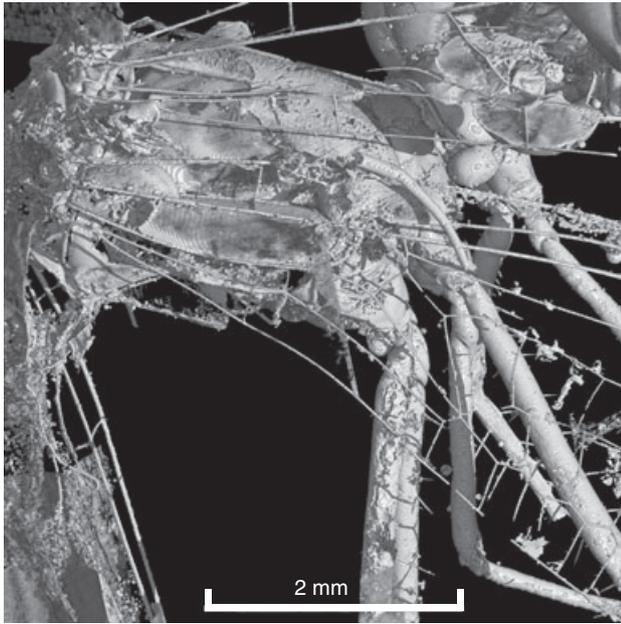


Figure 9. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, base of hindwing.

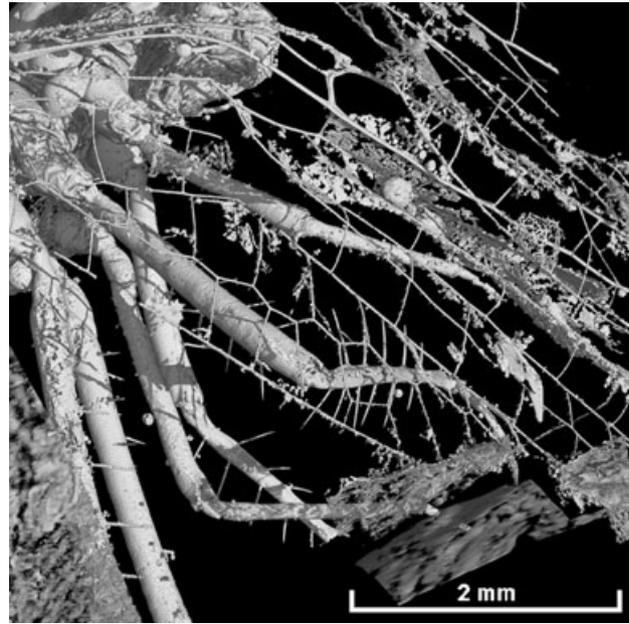


Figure 11. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, nodal region of hindwing.

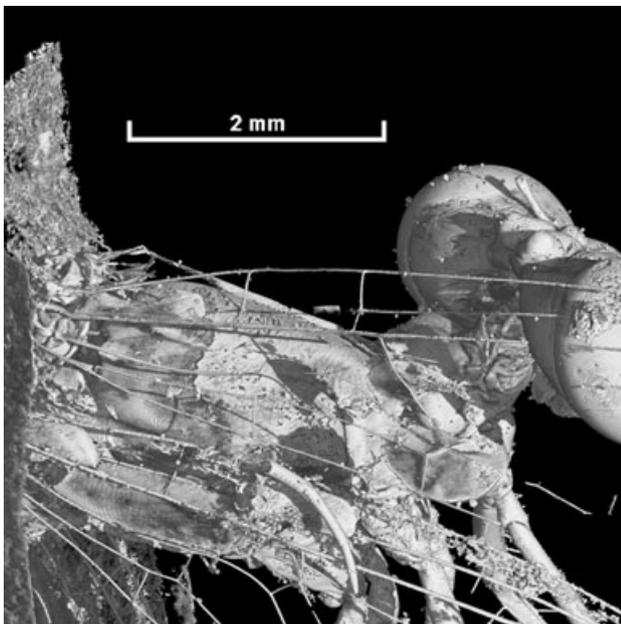


Figure 10. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, base of forewing.

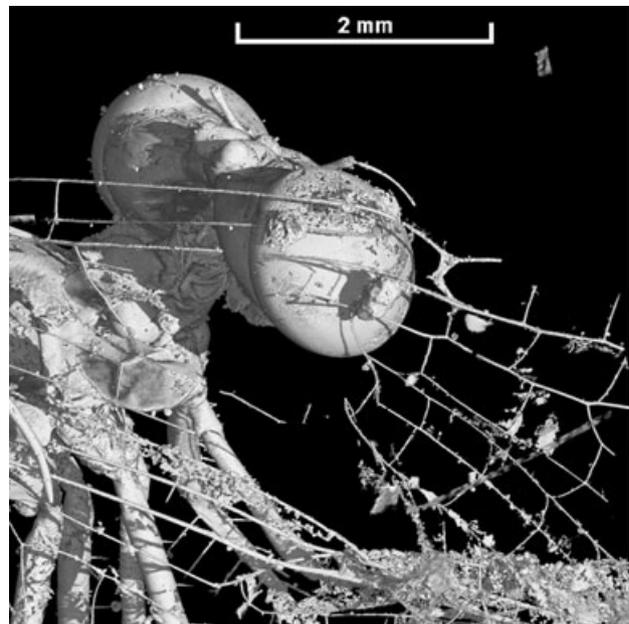


Figure 12. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, nodal region of forewing.

Type locality: Archingeay-Les Nouillers; Charente-Maritime; south-west France; Mid Cretaceous; Uppermost Albian (lithological subunit A1 *sensu* Néraudeau, Thierry & Moreau, 1997).

Diagnosis: As for the genus (*vide supra*).

Description: Forewing: petiole short, with AA separating from AP near wing base; one row of two long cells between AA and AP, between wing base and point of fusion between AA and CuA; CuP weakly curved, just distal cross-vein between two cells of anal area, between Ax1 and Ax2, but nearer level of Ax1 than that of Ax2, 0.2 mm distal of level of Ax1; no second-

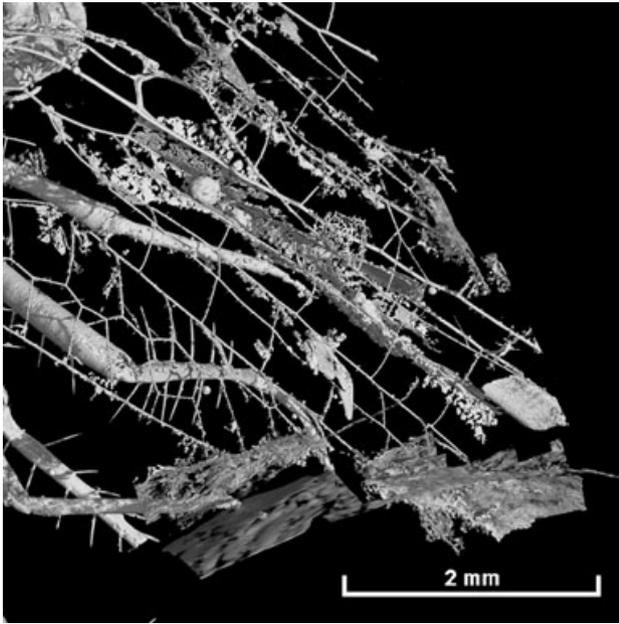


Figure 13. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, apical part of hindwing.

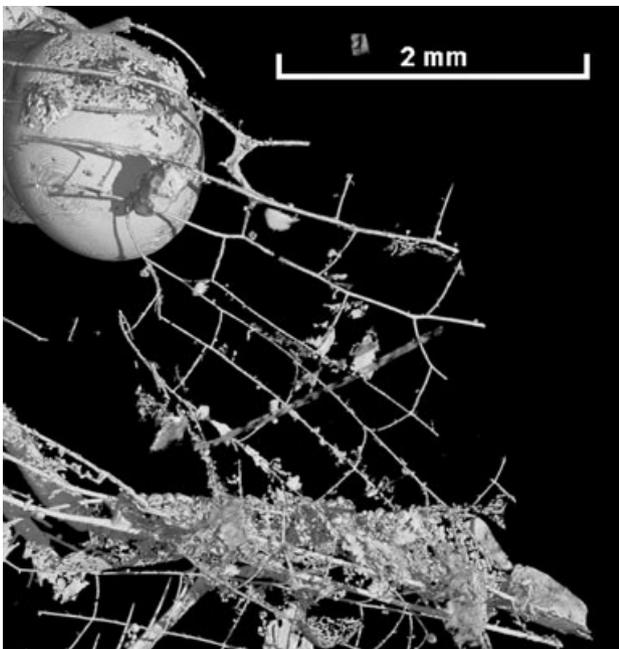


Figure 14. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1, apical part of forewing.

ary antenodal cross-vein; arculus 0.2 mm distal of Ax2; distance between wing base and Ax1 1.2 mm, between Ax1 and Ax2 0.8 mm; distance between wing base and nodus about 4.5 mm, between arculus and nodus 2.5 mm; median and submedian spaces free; discoidal cell basally opened; RP + MA, basal part of



Figure 15. *Hemiphlebia mirabilis* Selys, 1869, dorsal view of head.



Figure 16. *Hemiphlebia mirabilis* Selys, 1869, anterior view of head.

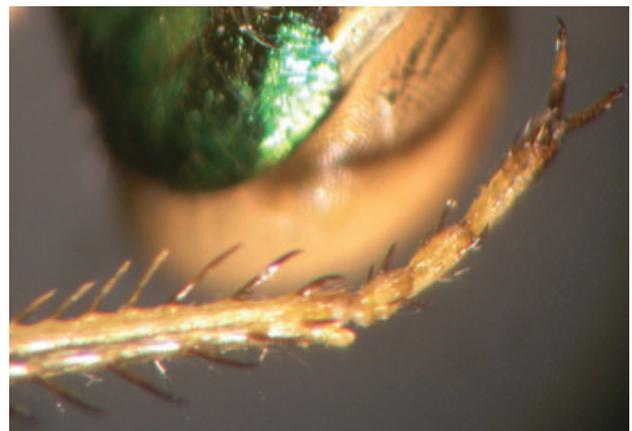


Figure 17. *Hemiphlebia mirabilis* Selys, 1869, ventral view of fore tibia.

MA and MAb aligned or nearly so; angle between MAb and MP + CuA rather acute in discoidal cell; MAb 0.5 mm long; basal part of MA 0.3 mm long; MP with a strong curve near its base; terminal kink of CP at nodus reduced; nodal Cr of normal obliquity; sub-nodus vertical; MP reaching posterior wing margin

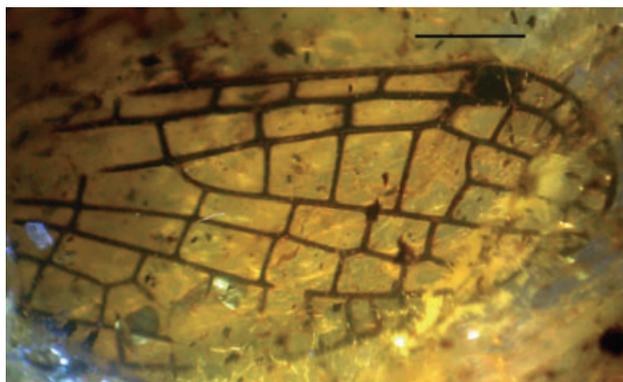


Figure 18. *Jordanhemiphlebia electronica* Kaddumi gen. et sp. nov., holotype, apical half of wing. Scale bar = 1 mm.

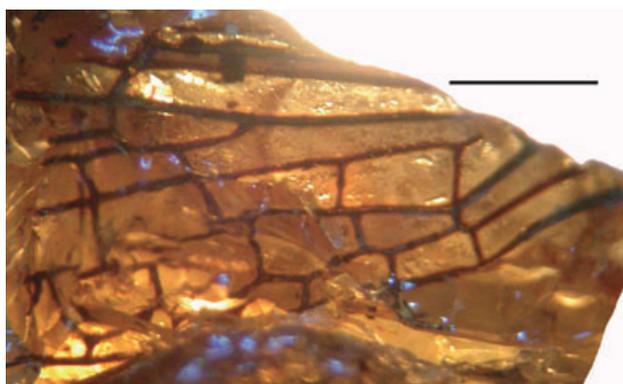


Figure 19. *Jordanhemiphlebia electronica* Kaddumi gen. et sp. nov., holotype, basal half of wing. Scale bar = 1 mm.

about two to three cells distal base of RP2; basal part of postdiscoidal area poorly preserved but probably one row of cells between MA and MP; base of RP3/4 between arculus and nodus, very close to nodus; base of IR2 opposite subnodus; one cell between base of RP3/4 and IR2; base of RP2 two cells distal of subnodus; subnodus apparently with a normal obliquity, not vertical; only two basal postnodal cross-veins and two basal postsubnodal cross-veins preserved, not aligned; no oblique cross-vein between IR2 and RP2.

Hindwing: petiole short, with AA separating from AP near wing base; one row of two long cells between AA and AP, between wing base and point of fusion between AA and CuA; CuP weakly curved, just distal cross-vein between the two cells of anal area, between Ax1 and Ax2, but nearer the level of Ax1 than that of Ax2, 0.3 mm distal of level of Ax1; distance between wing base and Ax1 1.5 mm, between Ax1 and Ax2 0.9 mm; no secondary antenodal cross-vein; arculus 0.2 mm distal of Ax2; median and submedian spaces free; discoidal cell basally

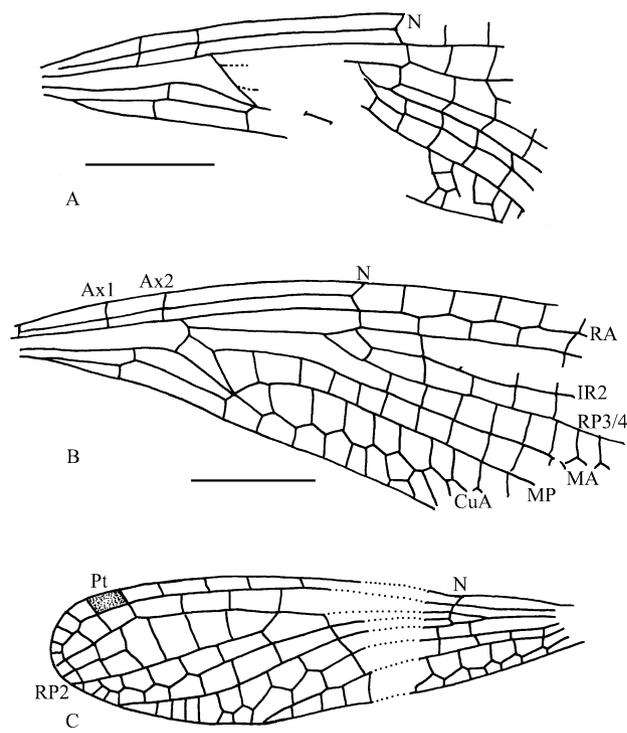


Figure 20. Wing reconstructions. A–B. *Electrohemiphlebia barucheli* gen. et sp. nov., holotype ARC 372.1. A, forewing. B, hindwing. C, *Jordanhemiphlebia electronica* Kaddumi gen. et sp. nov., holotype. Scale bars = 2 mm. N, nodus; Ax1, Ax2, primary antenodal cross-veins; RA, radius anterior; RP, radius posterior; IR, intercalary radial veins; MA, median anterior; MP, median posterior; CuA, cubitus anterior; Pt, pterostigma.

closed, with a distinct angle in MA at its point of contact with basal side of discoidal cell, and an angle between MA and MAb; basal part of MA (anterior side of discoidal cell) 0.5 mm long, MAb 0.8 mm long, posterior side 1.1 mm long, basal side 0.3 mm long; terminal kink of CP at nodus reduced; nodal Cr of normal obliquity; subnodus vertical; MP with a strong curve near its base; one row of cells between MA and MP and between MP and CuA; CuA strongly zigzagged in its distal part, with one to two rows of cells between it and posterior wing margin; base of RP3/4 between arculus and nodus, close to nodus; base of IR2 opposite nodal Cr and subnodus, 0.5 mm distal of base of RP3/4; area between RA and RP broadened at level of base of RP3/4; one cell between bases of RP3/4 and IR2; subnodus not visible; base of RP2 two cells distal of subnodus; no oblique cross-vein between IR2 and RP2; areas between RP3/4 and MA and between RP3/4 and IR2 both with one row of cells, distally broadening, but with distal part missing; pterostigma and pterostigmal brace not preserved.

Body: Head 3.68 mm wide; compound eye broad, 1.02 mm wide in frontal view; distance between eyes 1.65 mm, head not very transverse; antennal scape very strong, distinctly longer than wide, about twice as long as wide; pedicel well developed; flagellum reduced to a tiny bristle, 0.6 mm long; labrum weakly developed, gibbose, transverse, 0.3 mm long, 0.8 mm wide, with lateral margin rounded, mandibles well exposed; anteclypeus clearly visible, small, 0.1 mm long, 0.2 mm wide, postclypeus broader than labrum, 0.3 mm long, 1.0 mm wide; clypeo-frontal sulcus deeply impressed; anterior part of frons with two strong gibbositities separated by a median depression; antennal insertions in lateral position relative to the antefrons, not aligned with front ocellus; a strong sulcus between frons and vertex; posterior ocelli on a high gibbosity well separated from others by strong depressions; lateral sulci between ocelli and lateral sides of vertex complete and reaching posterior sulcus of the vertex; suture between vertex and occiput rather well pronounced. All legs preserved at least in part, with two rows of strong spines on femora and tibiae; protibial comb absent; profemur 1.3 mm in length, protibia c. 1.6 mm in length; mesofemur 1.8 mm in length, mesotibia 1.7 mm in length, tarsi 0.4 mm in length; metafemur 3.1 mm in length, metatibia not preserved; three tarsomeres on all legs. Lateral neck structure of arrester system *sensu* Gorb (1998) well visible (arrester system present) (Fig. 12); prothorax with notal anterior lobe narrow but rather pronounced anterior margin, median notal lobe broad, with two low lateral gibbositities separated by a median depression, posterior notal lobe well defined, erected and in dorsal view bearing a small triangular lug at median part of distal border (Figs 5, 12); area constituted by anterior margin of pterothorax and collar crests delimiting a well-defined triangle, larger than in *Hemiphlebia* (Fig. 5); pterothorax of zygopterid type, distinctly higher than wide, 2.7 mm high, 2.0 mm wide; interpleural suture only present around metastigmal area, 0.3 mm in length, dorsal part absent.

Discussion: The presence of long and slender raptorial legs, with femoral spines similar to the tibial spines, and the reduction of the terminal kink of CP at the nodus are apomorphies of Zygoptera (Bechly, 1996). The transverse elongation, the dorsoventral median compression of the head capsule, and distance between the compound eyes of *Electrohemiphlebia barucheli* gen. et sp. nov. are comparable to those of many Zygoptera. The well-pronounced cephalic sulcus between the frons and vertex, as in *Hemiphlebia* (Figs 4, 16), is a feature unlike most Zygoptera.

Within the Zygoptera few taxa have so dissimilar discoidal cells in the fore- and hindwing, i.e. with the cell basally opened and with anterodistal part nearly straight in the forewing, but basally closed and with strong angles between the anterior and distal sides in the hindwing. This is especially true for the Recent Australian genera *Hemiphlebia* Selys, 1868 (Hemiphlebiidae Tillyard, 1926) and *Chorismagrion* Morton, 1914 (Chorismagrionidae Tillyard & Fraser, 1938), and also the Early Cenozoic family Frengueliidae Petrulėvičius & Nel, 2003 (Petrulėvičius & Nel, 2003, 2007). The latter strongly differs from *Electrohemiphlebia* in the bases of RP3/4 and IR2 being well basal of the nodus and in having a very different, highly specialized nodus. *Chorismagrion* differs from *Electrohemiphlebia* in that its postnodal and postsubnodal cross-veins are aligned, the wings have a long petiole, and the arculus is just distal to Ax2 (Münz, 1919). *Electrohemiphlebia* differs from *Hemiphlebia* in AA separating from AP very close to the wing base, instead of close to the level of CuP, and the vertical subnodus.

Bechly (1996), after Kennedy (1919), proposed as a synapomorphy of *Hemiphlebia* the obsolescence of the protibial comb, a feature also seen in *Electrohemiphlebia* (Figs 6, 17). Furthermore, *Electrohemiphlebia* and *Hemiphlebia* share the presence of a sulcus between the frons and vertex; posterior ocelli positioned on pronounced gibbositities (although certainly more pronounced in *Electrohemiphlebia* than in *Hemiphlebia*); and complete and deep sulci between ocelli, ocellar gibbositities, and lateral sides of postfrons (see Figs 5, 15) (Fraser, 1955). In the great majority of other recent Zygoptera the posterior ocelli are not placed on such pronounced gibbositities. There are no clear sulci between the ocelli and the lateral parts of the vertex, except in a few recent taxa (*Synlestes*). Such sulci are present in the Tarsophlebiidae, sister group of (Zygoptera + Epiproctophora) (visible in a specimen from China, Huang & Nel, 2009), but also in the Epiproctophora themselves (*Epiophlebia* and the Anisoptera). Accordingly, they are probable plesiomorphies of the taxa considered herein.

Electrohemiphlebia and *Hemiphlebia* also share a strongly reduced thoracic interpleural suture (only present in the metastigmal area in *Electrohemiphlebia*, but also present in the dorsal one-tenth in *Hemiphlebia*) (Asahina, 1957). Trueman (1999) considered the open discoidal cell of the forewing in *Hemiphlebia* to be 'derived with respect to the closed condition in Zygoptera'. This character could be considered a synapomorphy of *Electrohemiphlebia* and *Hemiphlebia*, but it is also present in some other Zygoptera that are not related to *Hemiphlebia*. Further characters shared by *Electrohemiphlebia* and *Hemiphlebia* are as follows: postnodal and post-

subnodal cross-veins not aligned (a symplesiomorphy after Bechly, 1998b); bases of RP3/4 and IR2 opposite the subnodus; CuA strongly zigzagged; arculus distinctly distal to Ax2, not opposite it; no secondary antenodal cross-veins; area between RA and RP broadened at level of base of RP3/4; all intercalary veins (except IR1? and IR2) suppressed (potential synapomorphy after Bechly, 1998b), petioles of wing base relatively reduced (potential synapomorphy after Bechly, 1998b).

Bechly (1998b) considered that the Early Cretaceous genus *Parahemiphlebia* Jarzembowski *et al.* (1998) was a hemiphlebiid, and that the other Early Cretaceous genus *Cretarchistigma* Jarzembowski *et al.* (1998) could also belong to this family. *Electrohemiphlebia* shares with both of these genera a similar pattern in the wing base, with AA separating from AP near the wing base, and two long cells in the anal area, in addition to similar overall patterns in the wing venation. *Electrohemiphlebia* differs from both *Cretarchistigma* and *Parahemiphlebia* in that the subnodus is vertical, rather than of more typical obliquity. A vertical subnodus is not frequent among Zygoptera, convergently present in two fossil clades, the Sieblosiidae and Dysagrioninae. *Electrohemiphlebia* differs also from *Cretarchistigma* in that the hindwing discoidal cell has its anterior margin distinctly shorter than the distal margin Jarzembowski *et al.* (1998). *Parahemiphlebia* comprises three species – *Parahemiphlebia cretatica* Jarzembowski *et al.*, 1998, *Parahemiphlebia mickoleiti* Bechly, 1998b (both from the Late Aptian, Crato Formation of north-eastern Brazil), and *Parahemiphlebia allendaviesi* Jarzembowski *et al.*, 1998 (Berriasian Purbeck Group of the UK). The differences between the preserved and comparable wing venational structures of *Electrohemiphlebia* and these three species are few and at most of specific importance. In *P. allendaviesi*, the hindwing discoidal cell is shorter than in *Electrohemiphlebia*. The wings of *P. mickoleiti* are exceedingly short, 9 mm in length, and distinctly shorter than those of *Electrohemiphlebia*. Distances from the base to the nodus are 3.7 mm in *P. mickoleiti*, 6.6 mm in *P. cretatica*, 5.3 mm in *P. allendaviesi*, and 4.5 mm in *Electrohemiphlebia*. Thus *Electrohemiphlebia* is only slightly larger than the smallest damselfly, *P. mickoleiti*. Lastly, *Electrohemiphlebia* differs from *P. cretatica* and *P. mickoleiti* in the distinctly narrower discoidal cell, with a more acute angle between MAb and MP + CuA (condition unknown for *P. allendaviesi*).

The discovery of *Electrohemiphlebia* confirms the former attribution of the genus *Parahemiphlebia* (based on wing venation only) to the Hemiphlebiidae and the very wide distribution (Brazil, UK, France, Jordan) of this family during the Cretaceous.

JORDANHEMIPHLEBIA KADDUMI GEN. NOV.

Etymology: The new genus-group name is a combination of Jordan and *Hemiphlebia*, type genus of the family. The name is feminine.

Type species: *Jordanhemiphlebia electronica* Kaddumi sp. nov.

Diagnosis: Very small damselflies; hindwing discoidal cell basally closed; base of RP3/4 close to subnodus; base of IR2 opposite subnodus; cell between bases of RP3/4 and IR2 very broad below subnodus; subnodus oblique; pterostigmal brace oblique but not aligned with basal part of RP1; IR1 very short; area between C and RA distal of pterostigma short.

JORDANHEMIPHLEBIA ELECTRONICA KADDUMI GEN. ET SP. NOV. (FIGS 18, 19, 20C)

Etymology: The specific epithet is based on the Greek term *elektron* (meaning, 'amber').

Material: Holotype specimen deposited in Eternal River Museum of Natural History, Amman, Jordan.

Type locality: Wadi Zerqa; Jordan; Lower Cretaceous; Barremian.

Diagnosis: As for the genus (*vide supra*).

Description: Wing hyaline, petiole not preserved but after rather broad anal area with AA parallel to AP, petiole probably quite short, with AA separating from AP near wing base, and not below CuP; one long cell between AA and AP, below discoidal cell and Ax1 and basal of point of fusion between AA and CuA; Ax1 and Ax2 not preserved, no secondary antenodal cross-vein; distance between apex of discoidal cell and nodus 2.4 mm, discoidal cell basally closed; MAb 0.5 mm long; MP not strongly curved near its base; terminal kink of CP at nodus reduced; nodal Cr of normal obliquity; subnodus nearly vertical; CuA strongly zigzagged, reaching posterior wing margin opposite subnodus; one row of cells in cubito-anal area; MP straight, reaching posterior wing margin one cell distal base of RP2; one row of cells between MA and MP; MA distally zigzagged; base of RP3/4 between arculus and nodus, very close to nodus; base of IR2 opposite subnodus; one large cell between base of RP3/4 and IR2; base of RP2 two cells distal of subnodus; five postnodal cross-veins not aligned with four postsubnodal cross-veins; no oblique cross-vein between IR2 and RP2; IR1 very short, between pterostigma and wing apex; RP1 with a strong angle below pterostigmal brace; pterostigmal brace strong

and oblique; pterostigma covering one cell, 0.6 mm long, 0.3 mm wide; only four cells between C and RA distal of pterostigma.

Discussion: This wing is nearly identical to the hindwings of the Cretaceous hemiphlebiid genus *Parahemiphlebia*, the only difference being the weaker obliquity of the pterostigmal brace, which is not aligned with the proximal portion of RP1 (Bechly, 1998b; Jarzembowski *et al.*, 1998). The second hemiphlebiid genus *Cretarchistigma* differs from *Jordanhemiphlebia* in the longer vein IR1 that begins two cells basal to the pterostigma, instead of below the pterostigma as in *Jordanhemiphlebia* and *Parahemiphlebia*. *Jordanhemiphlebia* differs from the third Cretaceous hemiphlebiid genus, *Electrohemiphlebia*, in the nodal Cr and subnodus of normal obliquity, instead of being vertical. Lastly, *Jordanhemiphlebia* differs from *Hemiphlebia* in the shorter IR1, shorter area between C and RA distal of pterostigma, broader cell between the bases of RP3/4 and IR2 below the subnodus, and probably AA separating from AP very close to the wing base, instead of close to the level of CuP (Münz, 1919).

CONCLUSION

The hemiphlebiid damselflies were widespread in the Early Cretaceous and the family is likely to be quite ancient, dating from the Late Jurassic or even earlier. Hemiphlebiid damselflies were apparently dominant among Zygoptera in the Early Cretaceous. They perhaps occupied the ecological niches of the small to very small damselflies. They are at present replaced everywhere by coenagrionoids, except in a few areas in extreme south-east Australia and Tasmania where *Hemiphlebia* is still living.

Whereas the oldest true Odonata are of Late Permian age and the earliest Epiroctophora (sister group to Zygoptera) are from the Late Triassic, curiously the oldest documented damselflies are from the Late Jurassic (Nel *et al.*, 1999; Fleck *et al.*, 2001). This gap is most probably not owing to taphonomic effects because some Jurassic damsel-dragonflies were as slender and fragile as true damselflies, although others were certainly more robust. The latter clade probably began to diversify in the Late Jurassic, and may have been represented solely by stem-group families in the Triassic and earliest Jurassic.

Damselflies certainly co-existed with the slender damsel-dragonflies from the Late Triassic and Late Jurassic, whereas the robust damsel-dragonflies persisted into the Early Cretaceous and are represented in the modern fauna by the relic family Epiophlebiidae. These lineages also co-existed with the protozy-

gopteran Protomyrmeleontidae, a strange family that lived from the Late Triassic to the end of the Early Cretaceous (Nel, Petrulevičius & Martínez-Delclòs, 2005). The diversification of the damselflies and extinction of other 'damselfly-like' Odonata was certainly not related to the better flight performances of the former as the flight structures of all these insects are fundamentally the same (i.e. very elongate thoraces and long, petiolate, and narrow wings). Birds diversified during the Cretaceous as a new group of small aerial predators, but their impact on all these insects of nearly the same size and flight performance was certainly not sufficient to discriminate amongst all these 'damselfly-like' Odonata. Nothing is known of the aquatic immatures or how changes in freshwater palaeoenvironments (e.g. chemistry, temperature) during the Early Cretaceous may have played into their disappearance, a factor that probably caused the extinction of the strongly diversified and worldwide distributed Mesozoic family Aeschniidae, also of the Odonata (Fleck & Nel, 2003).

ACKNOWLEDGEMENTS

This work was supported by the French Research Agency (ANR), project 'AMBRACE' n° BLAN07-1-184190, and the European Synchrotron Radiation Facility (ESRF) of Grenoble. This paper is a contribution to the project 'The Study of the Fossil Insects and their Outcrops: Geology of the Outcrops – Historical and Biodiversity Evolution' accorded by the Lebanese University to DA. The authors warmly thank Simon Defortis for his participation in the 3D imaging of the Zygoptera and J. Baruchel, from the beamline ID19 of the ESRF, for his invaluable help.

REFERENCES

- Asahina S. 1957.** On the pterothoracic interpleural suture of Mesozoic and Recent Odonata. *Journal of the Faculty of Sciences Hokkaido University, Zoology* **13**: 1–7.
- Bechly G. 1996.** Morphological studies of the wing venation of the recent Odonata and their stemgroup (Insecta; Pterygota; Odonata), with an analysis of the phylogenetic systematic and groundplan of the Odonata. *Petalura, Böblingen, Special Volume* **2**: 1–402.
- Bechly G. 1998a.** New fossil damselflies from Baltic amber with description of a new species, a redescription of *litheuphae carpenteri* Fraser, and a discussion on the phylogeny of Epallagidae. *International Journal of Odonatology* **1**: 33–63.
- Bechly G. 1998b.** New fossil dragonflies from the Lower Cretaceous Crato Formation of North-East Brazil (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde, Serie B, Geologie und Paläontologie* **264**: 1–66.

- Brenner GJ, Bickoff IS. 1992.** *Palynology* and age of the Lower Cretaceous Basal Kurnub Group from the coastal plain to the Northern Negev of Israel. *Palynology* **16**: 137–185.
- Fleck G, Nel A. 2003.** Revision of the Mesozoic family Aeschnidiidae (Odonata: Anisoptera). *Zoologica* **153**: 1–172.
- Fleck G, Nel A, Bechly G, Martínez-Delclòs X. 2001.** Revision and phylogenetic affinities of the Jurassic Steleopteridae Handlirsch, 1906 (Insecta: Odonata: Zygoptera). *Insect Systematic Evolution* **32**: 285–305.
- Fraser FC. 1955.** A study of *Hemiphlebia mirabilis* Selys (Odonata), a survival from the Permian. *Entomologists' Monthly Magazine* **91**: 110–113.
- Gorb SN. 1998.** Functional morphology of the head-arrester system in Odonata. *Zoologica* **148**: 1–132.
- Huang D-Y, Nel A. 2009.** The first Chinese Tarsophlebiidae from the Lower Cretaceous Yixian Formation, with morphological and phylogenetic implications (Odonatoptera: Panodonata). *Cretaceous Research* **30**: 429–433.
- Jarzembowski EA, Martínez-Delclòs X, Bechly G, Nel A, Coram R, Escullié F. 1998.** 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, Hemiphleboidea, Lestoidea). *Cretaceous Research* **19**: 403–444.
- Kaddumi HF. 2005.** *Amber of Jordan. The oldest prehistoric insects in fossilised resins*. Jordan: Eternal River Museum of Natural History.
- Kennedy CH. 1919.** The phylogeny of the Zygoptera. PhD thesis, Cornell University, Ithaca, N.Y.
- Lak M, Néraudeau D, Nel A, Cloetens P, Perrichot V, Tafforeau P. 2008.** Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. *Microscopy and Microanalysis* **14**: 251–259.
- May ML, Carle FL. 2005.** *Pamita hannahdaltonae* gen. nov., sp. nov. from Baltic amber (Odonata : Amphipterygida). *International Journal of Odonatology* **8**: 213–221.
- Münz PA. 1919.** A venational study of the suborder Zygoptera (Odonata) with keys for the identification of genera. *Memoirs of the Entomological Society of the Academy of Natural Sciences* **3**: 1–78.
- Nel A, Arillo A. 2006.** The first Baltic amber dysagrionine damselfly (Odonata: Zygoptera: Thaumatoeuridae: Dysagrioninae). *Annales de la Société Entomologique de France* **42**: 179–182.
- Nel A, Gand G, Fleck G, Bethoux O, Lapeyrie J. 1999.** *Saxonagrion minutus* nov. gen. et sp., the oldest 'damselfly' from the Upper Permian of France (Odonatoptera, Panodonata, Saxonagrionidae nov. fam.). *Geobios* **32**: 883–888.
- 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, Néraudeau D, Perrichot V, Girard V, Gomez B. 2008.** A new dragonfly family from the Upper Cretaceous of France. *Acta Palaeontologica Polonica* **53**: 165–168.
- Nel A, Petrulėvičius JF, Martínez-Delclòs X. 2005.** New Mesozoic Protomyrmeleontidae (Insecta: Odonatoptera: Archizygoptera) from Asia with a new phylogenetic analysis. *Journal of Systematic Palaeontology* **3**: 187–201.
- Néraudeau D, Perrichot V, Dejax J, Masure E, Nel A, Philippe M, Moreau P, Guillocheau F, Guyot T. 2002.** Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios* **35**: 233–240.
- Néraudeau D, Thierry J, Moreau P. 1997.** Variation in echinoid biodiversity during the Cenomanian-early Turonian transgressive episode in Charentes (France). *Bulletin de la Société géologique de France* **168**: 51–61.
- Petrulėvičius JF, Nel A. 2003.** Frenguelliidae, a new family of dragonflies from the earliest Eocene of Argentina (Insecta: Odonata): phylogenetic relationships within Odonata. *Journal of Natural History* **37**: 2909–2917.
- Petrulėvičius JF, Nel A. 2007.** Enigmatic and little known Odonata (Insecta) from the Paleogene of Patagonia and northwest Argentina. *Annales de la Société Entomologique de France* **43**: 341–347.
- Riek EF. 1976.** A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum* **22**: 791–820.
- Riek EF, Kukalová-Peck J. 1984.** A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. *Canadian Journal of Zoology* **62**: 1150–1166.
- Tafforeau P, Boistel R, Boller E, Bravin A, Brunet M, Chaimanee Y, Cloetens P, Feist M, Hoszowska J, Jaeger J-J, Kay RF, Lazzari V, Marivaux L, Nel A, Nemoz C, Thibault X, Vignaud P, Zabler S. 2006.** Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Applied Physics A, Materials Science & Processing* **83**: 195–202.
- Trueman JWH. 1999.** The enigmatic Australian endemic species *Hemiphlebia mirabilis* Selys, four short observations and a new record. *International Journal of Odonatology (Special Issue)* **2**: 115–121.