

New Paleogene Epallagidae (Insecta: Odonata) recorded in North America and Europe. Biogeographic implications

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ABSTRACT

Three new fossil Epallagidae: Eodichrominae are described, viz. *Labandeiraia* n. gen. with the two species *L. americaborealis* n. sp. (Eocene of USA), and *L. europae* n. sp. (Paleocene/Eocene of Denmark), and *Litheuphaea coloradensis* n. sp. (Eocene of USA). The pattern of distribution of this damselfly group in the Paleogene of North America and Europe is the same as for the damselfly subfamily Thaumtoneuridae: Dysagrioninae and the neuropteran Polystoechotidae. This pattern could correspond to Paleocene/Eocene land bridges between these continents via Greenland or Bering or to ancient Late Cretaceous groups.

KEY WORDS: Insecta. Odonata. Epallagidae. New genus, new species. Eocene. Biogeography.

INTRODUCTION

The recent distribution of the damselfly family Epallagidae ranges from the subtropical (incl. Mediterranean and Middle East regions) to the intertropical regions of Eurasia (Indo-Malayan region). Its fossil record comprises an Italian Late Miocene representative of the recent genus *Epallage* (Cavallo & Galletti 1987), and several Paleogene species from Europe and North America (Nel 1988, Bechly 1998). We describe one new genus and three new species of Epallagidae from North America and Denmark, increasing our knowledge on the diversity and distribution of this group during the Eocene.

We follow the wing venation nomenclature of Riek & Kukalová-Peck (1984), amended by Kukalová-Peck (1991), Nel *et al.* (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters followed in the present work are based on the phylogenetic system proposed by Bechly (1996).

SYSTEMATIC PALAEONTOLOGY

Order: Odonata Fabricius, 1793

Family: Epallagidae Needham, 1903

Subfamily: Eodichrominae Cockerell, 1923

GENUS: *Labandeiraia* n. gen.

Type species: *Labandeiraia americaborealis* n. sp. Other species: *Labandeiraia europae* n. sp.

Etymology. After our colleague Dr. Conrad C. Labandeira (Smithsonian Institution, National Museum of Natural History, Washington D. C., USA).

Diagnosis. Numerous antenodal cross-veins of first and second rows (more than 20); primary antenodal cross-veins stronger than secondaries and without secondaries between them; arculus opposite Ax2; discoidal cell elongate and narrow; anal area very broad and crossed by very long and narrow transverse cells; cubito-anal area very broad and with six long secondary longitudinal veins (three convex and three concave); more than two rows of cells between C and RA distal of pterostigma and between RA and RP1 below it; no pterostigmal brace; at least two long secondary longitudinal veins between all main veins.

Labandeiraia americaborealis n. sp.

Plate 1

Material. Holotype specimen 31.665A-B, Smithsonian Institution, National Museum of Natural History, USA, David Kohls, collector.

Etymology. After North America.

Age and outcrop. Eocene, Green River Formation, Parachute Creek Member, Colorado, USA.

Diagnosis. Anal area broad, a basal curving of RP1/2, pterostigma covering 10 cells, 2-3 clear secondary longitudinal veins between MP and CuA.

Description. Print and counterprint of a complete single wing, completely dark brown, 41.5 mm long, 14.4 mm

wide, very broad and divided into numerous small cells; distance from base to arculus 3.1 mm, from arculus to nodus 10.2 mm, from nodus to pterostigma 19.8 mm, from pterostigma to wing apex 4.7 mm; pterostigma 4.9 mm long, 1 mm wide, covering 10 cells disposed in 2-3 rows, basal side of pterostigma very oblique, more oblique than distal side, pterostigmal brace absent; wing petiole absent, anal area broad, with large and narrow transverse cells, 0.35 mm wide in its middle; median area free of cross-veins; submedian area free of cross-vein in its basal half but with vein CuP and few other cross-veins in its distal half; discoidal cell elongate and narrow, 3.3 mm long, 0.4 mm wide, apparently crossed by a transverse vein in its middle; no antefurcal cross-veins between basal parts of RP and MA; primary antenodal cross-veins Ax1 and Ax2 stronger than secondary antenodals, Ax1 2 mm from wing base, distance between Ax1 and Ax2 1.1 mm, no secondary antenodal cross-vein between Ax1 and Ax2; arculus opposite Ax2; 23 secondaries of first row between Ax2 and nodus and numerous secondaries of the second row, but these are more poorly preserved and probably not all visible; kink of ScP at nodus very abrupt and Z-like; subnodus aligned with nodal cross-vein Cr; base of RP3/4 1.5 mm from arculus, base of IR2 only 1.3 mm distally; basal curving of RP1/2; numerous cross-veins in antesubnodal area; postdiscoidal area with only one row of cells between discoidal cell and nodus level, but greatly widened distally, and with two long secondary longitudinal veins; area between MP and CuA progressively broadened and with two long secondary longitudinal veins; CuA not forked; cubito-anal area very broad, 6.2 mm wide in its broadest part, and with three long concave and three long convex secondary longitudinal veins; anal area distinctly broader than distance between postero-distal angle of the subdiscoidal cell and costal wing margin; area between MA and RP3/4 narrow between arculus and nodus but distally broadened with two long secondary longitudinal veins; area between RP3/4 and IR2 progressively broadened, with two long secondary longitudinal veins; base of RP2 aligned with subnodus; base of IR1 close to that of RP2; IR1, RP2, IR2, and RP3/4 rather straight and faintly curved near their apices; more than 45 postnodal cross-veins and postsubnodal cross-veins; 3-4 rows of cells between Costa and RA distal of pterostigma; three rows of cells between RA and RP1 and between RP1 and IR1.

Discussion. *Labandeiraia* n. gen. falls in the Calopterygo-morpha Bechly (1996) because of the following characters: antenodal area with very numerous antenodal cross-veins that are very close together; kink of ScP at nodus very abrupt and Z-like; strong tendency towards a basal curving of RP1/2 which seems to arise on RP with a secondary insertion; strong tendency towards an elongation of the discoidal cell and its subdivision by cross-veins. It can be included in the Calopterygiformia Bechly (1996) rather than the Chlorocyphoidea Cowley (1937) because it has not the synapomorphies of the latter clade, viz. discoidal cell extremely elongated; only one row of cells

between MP and CuA and between CuA and the hind margin; RP3/4 waving and MA distinctly upward curved immediately after the discoidal cell, even if it has not the unique wing venational synapomorphy of the former, as for the other Eodichrominae, i.e. the presence of basal accessory antenodal cross-veins between Ax0 and Ax1. It falls in the Euphaeida Bechly (1996) for the following synapomorphies: strongly developed dorsal discoidal bracket on the distal side MAb of the discoidal cell and on the subdiscoidal veinlet (basal CuA). Within this clade, it has not the synapomorphies of the Polythoridae Munz (1919), viz. discoidal cell touches RA, because the arculus is only formed by the basal discoidal cross-vein (= posterior arculus) that is developed as an apparent branch of [M & Cu]; dorsal arcular bracket reduced; median space traversed by numerous cross-veins; submedian space traversed by numerous cross-veins; discoidal cell traversed by several cross-veins; anterior side of discoidal cell concave (MA basally curved), and basal side at least twice as long as distal side; CuA secondarily forked into CuAa and CuAb, with a concave intercalary vein between these branches. But it has the synapomorphies of the Epallagoidea Needham (1903): petiolus shortened (but convergent to Calopterygidae); distal discoidal vein MAb and subdiscoidal vein with reversed obliquity (but convergent to Calopterygidae); CuA sigmoidally and smoothly curved; curved intercalary veins between CuA and hind margin; [M & Cu] or MP not kinked or bent at arculus (but convergent to Calopterygoidea). These characters remain rather uncertain as they are also present in the Calopterygidae, but *Labandeiraia* n. gen. cannot be included in this last group because its CuA is not forked.

Within the Epallagoidea, *Labandeiraia* n. gen. cannot be included in the Zacallitidae Cockerell (1928) because its base of IR2 is not widely separated from midfork, and its discoidal cell is distinctly longer than wide (as long as wide in *Zacallites balli* Cockerell 1928). It can be attributed to the Epallagidae Needham (1903) on the basis of the two characters 'antenodal cross-veins distinctly more numerous than in *Zacallites*', and 'at least a smooth basal curving of RP1/2 towards RA'. The two other putative synapomorphies of this family are more dubious, i.e. 'arculus shifted basally between Ax2 and Ax1' cannot be determined in Epallaginae, and the character 'both rows of antenodal cross-veins strictly aligned' is absent in the genus *Litheuphaea* Fraser 1955. Both these characters are absent in *Labandeiraia* n. gen. This taxon can be attributed to the Eodichrominae Cockerell (1923) rather than to the Epallaginae Needham (1903) because it has not the synapomorphies of the latter, i.e. its base of IR2 is not widely separated from the midfork, its base of RP1/2 is less strongly curved towards RA, and its two primary antenodal brackets Ax1 and Ax2 can be distinguished from the secondary antenodal cross-veins, and it has the synapomorphies of the former clade, viz. cubito-anal area secondarily expanded, Ax1 and Ax2 closely approximated, and no antefurcal cross-veins between basal parts of RP and MA.

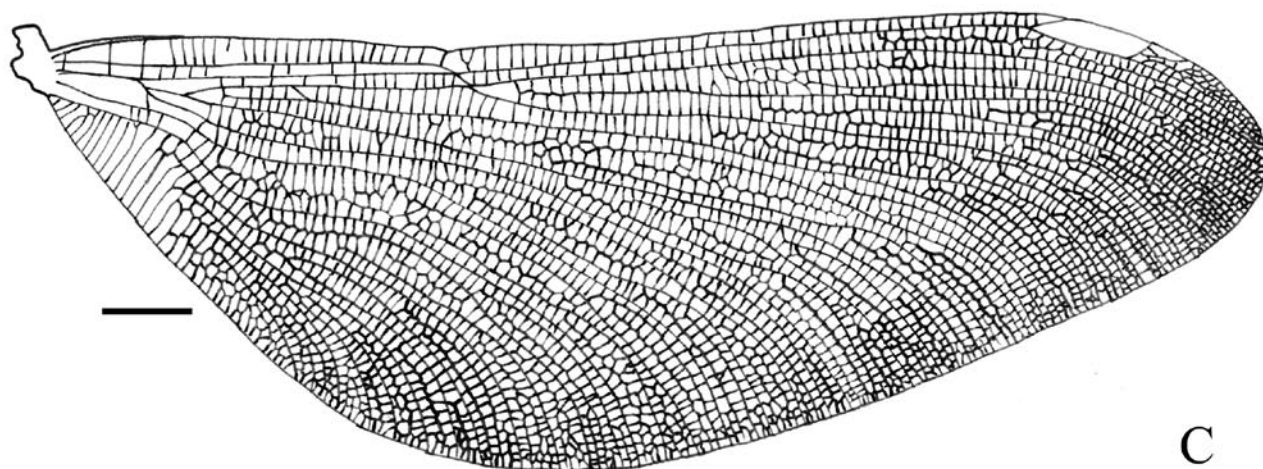
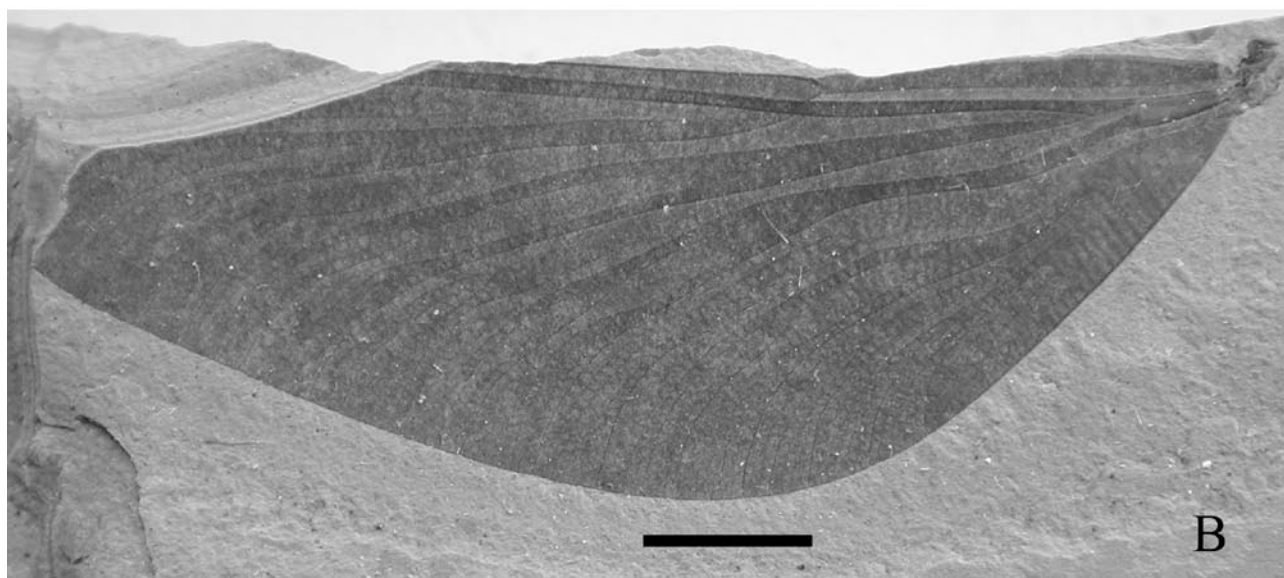
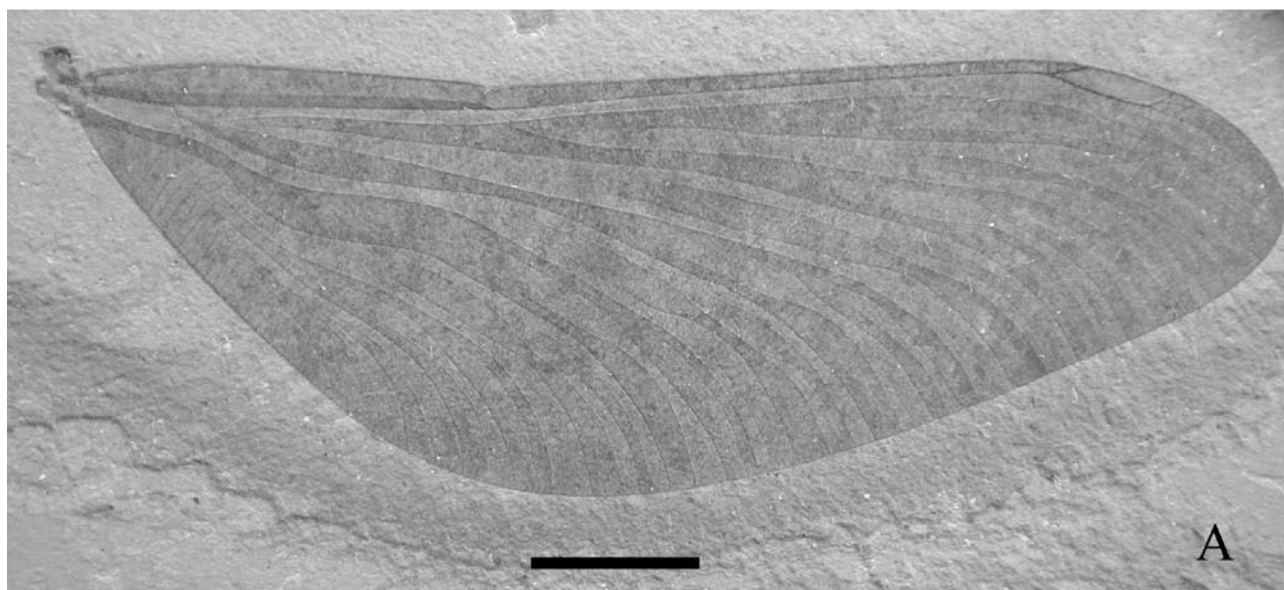


Plate 1. *Labandeiraia americaborealis* n. gen., n. sp., holotype. A, 31.665A, photograph of print. B, 31.665B, photograph of counterprint (scale bars represent 5 mm). C, 31.665A, drawing of wing (scale bar represents 3 mm).

Bechly (1998) proposed that the Eodichrominae had a unique accessory concave ‘anal’ vein (intercalary) between CuA and the hind margin, but it is not the case in *Labandeiraia* n. gen. Thus this character is no longer a synapomorphy of this clade.

Bechly (1998) divided this extinct subfamily into the two tribes Eodichromini Cockerell (1923) (*Eodichroma mirifica* Cockerell 1923 and *Parazacallites aquisextanea* Nel 1988), and Litheuphaeini Bechly (1996) (*Litheuphaea carpenteri* Fraser 1955 and *Litheuphaea ludwigi* Bechly 1998). *Labandeiraia* n. gen. differs from *Litheuphaea* in the presence of numerous secondary antenodal cross-veins between ScP and RA.

Eodichroma has a characteristic pattern of intercalary veins in the cubito-anal area that form an asymmetrical triadic fork with Cu, which is not present in *Labandeiraia* n. gen. Also, the cubito-anal area of *Labandeiraia* n. gen. is much broader than that of *Eodichroma*. *Parazacallites* has an arculus shifted basal to Ax1, unlike *Labandeiraia* n. gen. Therefore, the tribal attribution of *Labandeiraia* n. gen. is not clear at all, showing that the current classification of the Eodichrominae is not really satisfactory.

The fossil genus and species *Epallagites avus* Cockerell 1924 from the Eocene of Colorado (Green River) is based on a poorly preserved small fragment, currently regarded as a Zygoptera: Caloptera *incertae sedis* (Carpenter 1992, Nel & Paicheler 1992). It differs from *Labandeiraia* n. gen. in the presence of three antenodals basal of arculus and about 15 antenodals between arculus and nodus (Cockerell 1924: 9).

Labandeiraia europae n. sp.

Plates 2-3

1999 ‘Calopteryginae gen. et sp. indet.’, Rust, 20-22, text-fig. 5, pl. 1, fig. c.

Material. Holotype specimen MM 5-2902 (hindwing?), Moler Museum, Mors, Denmark; paratypes MM 1255 (forewing?) and In. 37782, British Museum of Natural History, London, UK.

Etymology. After Europe.

Age and outcrop. Lowermost Eocene, Fur- Formation (“Mo-clay”), diatomite, Denmark.

Diagnosis. *L. europae* n. sp. has few differences with the *L. americaborealis* n. sp., viz. anal area narrower, no basal curving of RP1/2, pterostigma covering 13 cells instead of 10, the double row of cells between RA and RP1 absent (forewing?) or beginning only four cells basal of the pterostigma instead of 14 cells (hindwing?), only one clear secondary longitudinal vein between MP and CuA, instead of 2-3 in *L. americaborealis* n. sp.

Description. Specimen MM 5-2902. A nearly complete wing, with extreme base missing, dark brown, probable wing length 44.2 mm, width 14.0 mm; distance from base to arculus unknown, from arculus to nodus about 9.2 mm, from nodus to pterostigma 22.3 mm, from pterostigma to wing apex 5.2 mm; pterostigma 4.7 mm long, 1.0 mm wide, covering about 10 cells disposed in 2 rows, basal side of pterostigma very oblique, more oblique than distal side, pterostigmal brace absent; wing petiole probably absent, anal area broad, with large and narrow transverse cells; median and submedian areas not preserved; discoidal cell elongate and narrow, 0.5 mm wide; subdiscoidal cell free; no antefurcal cross-veins between basal parts of RP and MA; primary antenodal cross-veins Ax1 and Ax2 not preserved; clearly more than 14 secondaries of first row between Ax2 and nodus and numerous secondaries of the second row, preserved in basal half of area, missing in distal half (preservation?); kink of ScP at nodus very abrupt and Z-like; subnodus aligned with nodal cross-vein Cr; base of RP3/4 distinctly closer to arculus than to nodus, base of IR2 only 0.5 mm distally; no basal curving of RP1/2; numerous cross-veins in antesubnodal area; postdiscoidal area with only one row of cells between discoidal cell and nodus level, but greatly widened distally, and with at least one long secondary longitudinal vein; area between MP and CuA progressively broadened and with two long secondary longitudinal veins; CuA not forked; cubito-anal area very broad, 4.2 mm wide in its broadest part, and with three long concave and three long convex secondary longitudinal veins; anal area 2.6 mm wide, narrower than distance between postero-distal angle of the subdiscoidal cell and costal wing margin; area between MA and RP3/4 narrow between arculus and nodus; area between RP3/4 and IR2 progressively broadened, with at least one long secondary longitudinal vein; base of RP2 aligned with subnodus; base of IR1 close to that of RP2; IR1, RP2, IR2, and RP3/4 rather straight and faintly curved near their apices; 50 postnodal cross-veins and postsubnodal cross-veins; 3-4 rows of cells between Costa and RA distal of pterostigma; three rows of cells between RA and RP1 and between RP1 and IR1.

Specimen In.37782. Print of two wings dark brown, partly overlapping, basal part of one (hind?) wing (wing 1), and apical part of other wing (wing 2), 21.8 mm long, 10.6 mm wide (but the wing is deformed), very broad and divided into numerous small cells; distance from base to arculus unknown, from arculus to nodus about 5.8 mm, from nodus to pterostigma unknown, from pterostigma to wing apex 3.3 mm (in wing 2); pterostigma 5.1 mm long, 0.9 mm wide, covering 13 cells disposed in 2-3 rows, basal side of pterostigma very oblique, more oblique than distal side, pterostigmal brace absent; wing petiole probably absent, anal area broad, with large and narrow transverse cells, 0.35 mm wide in its middle; median and submedian areas not preserved; discoidal cell elongate and narrow, 0.5 mm wide; no antefurcal cross-veins between basal parts of RP and MA; primary antenodal cross-veins Ax1 and Ax2 not preserved; clearly more than 14 secondaries of first row

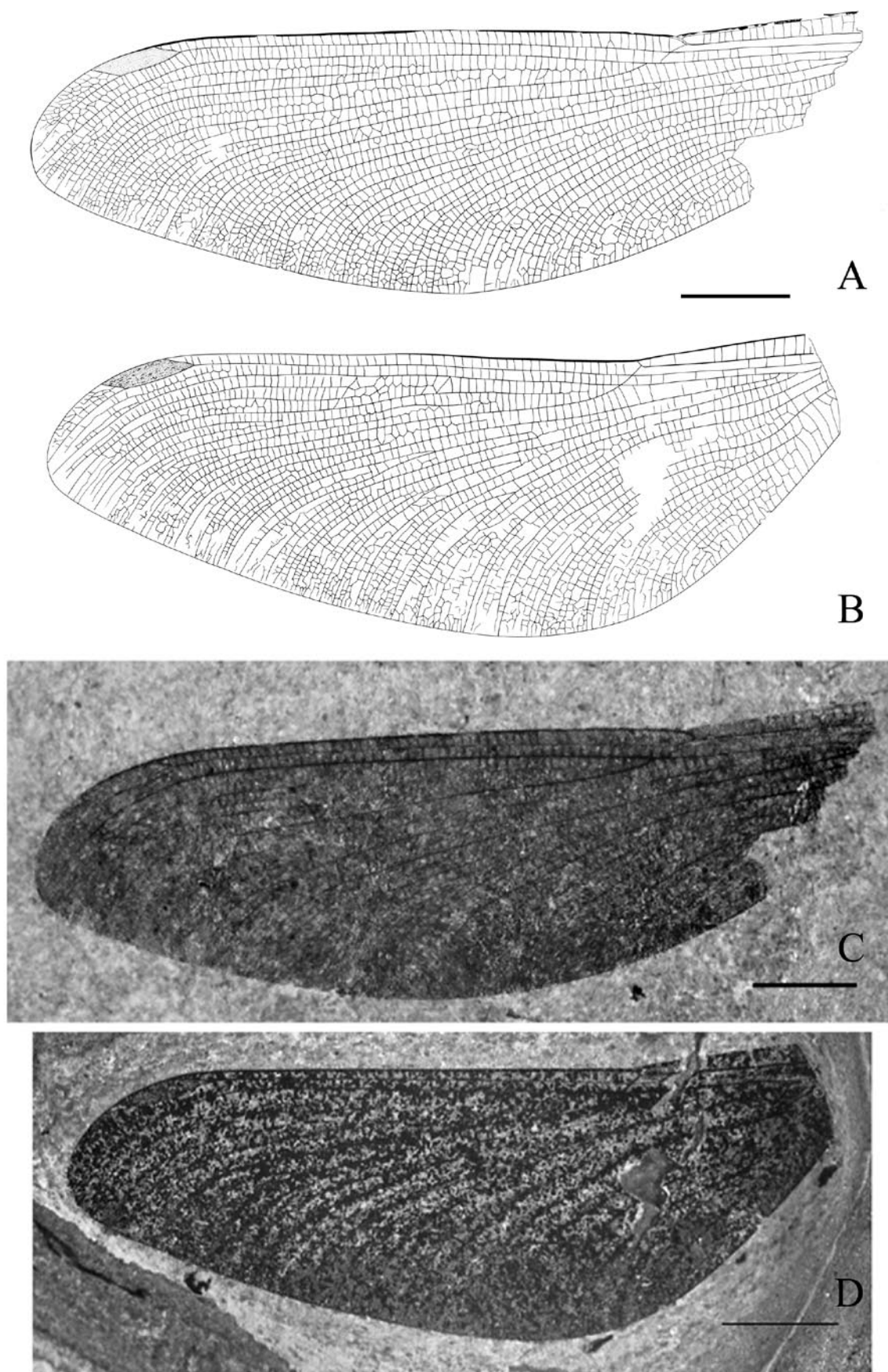


Plate 2. *Labandeiraia europae* n. sp., A, paratype MM 1255. B, holotype MM 5-2902, drawings of wings. C, MM 1255. D, MM 5-2902, photographs of wings (scale bars represent 5 mm).

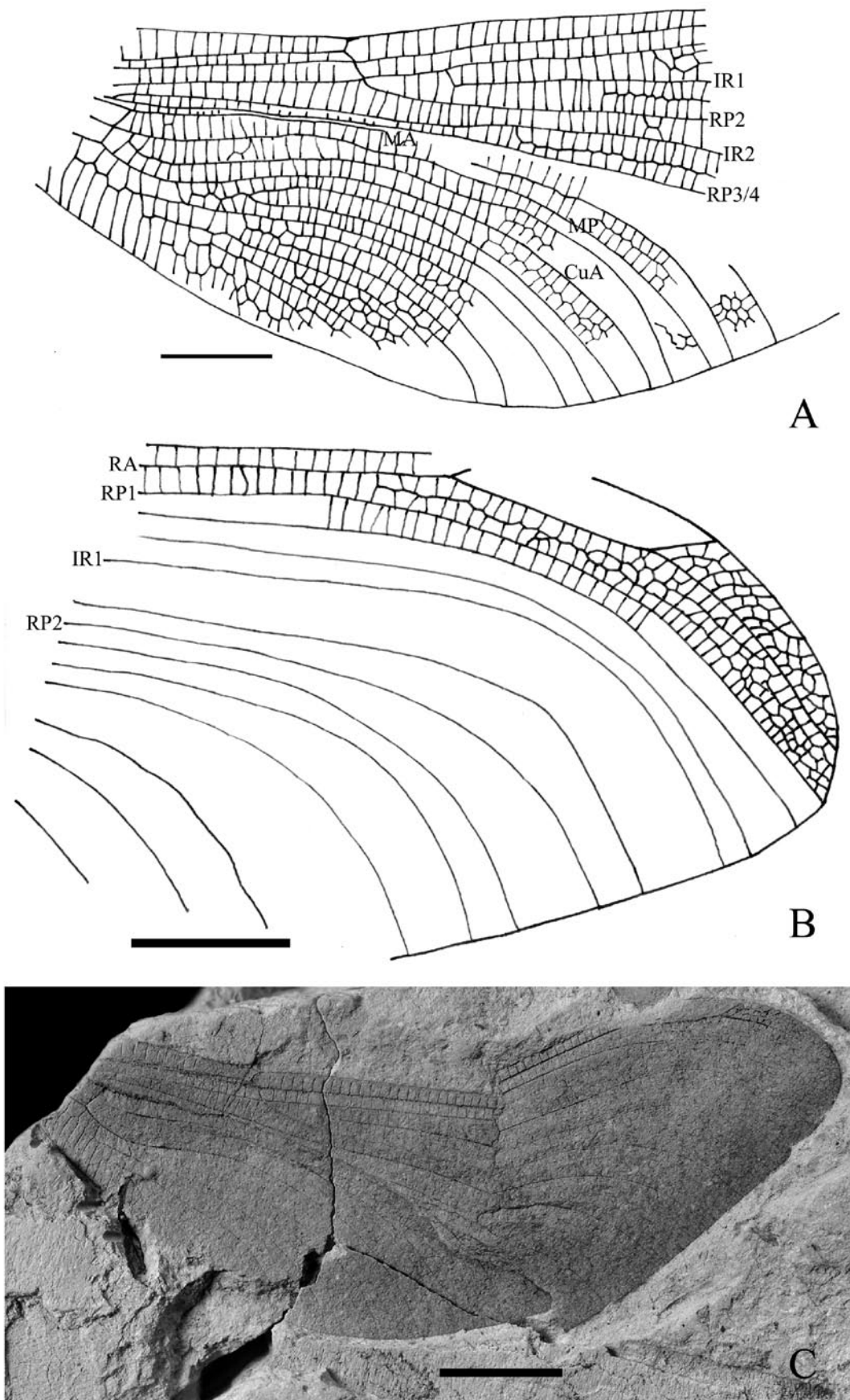


Plate 3. *Labandeiraia europae* n. sp., paratype In.37782. A, drawing of wing base. B, drawing of wing apex (scale bars represent 3 mm). C, photograph (scale bar represents 5 mm).

between Ax2 and nodus and numerous secondaries of the second row; kink of ScP at nodus very abrupt and Z-like; subnodus aligned with nodal cross-vein Cr; base of RP3/4 distinctly closer to arculus than to nodus, base of IR2 only 0.5 mm distally; numerous cross-veins in antesubnodal area; postdiscoidal area with only one row of cells between discoidal cell and nodus level, but greatly widened distally, and with at least one long secondary longitudinal vein; area between MP and CuA progressively broadened and with one long secondary longitudinal vein that begins just distal of discoidal cell; CuA not forked; cubito-anal area very broad, 5.9 mm wide in its broadest part, and with three long concave and three long convex secondary longitudinal veins; anal area 2.6 mm wide, narrower than distance between postero-distal angle of the subdiscoidal cell and costal wing margin; area between MA and RP3/4 narrow between arculus and nodus; area between RP3/4 and IR2 progressively broadened, with at least one long secondary longitudinal vein; base of RP2 aligned with subnodus; base of IR1 close to that of RP2; IR1, RP2, IR2, and RP3/4 rather straight and faintly curved near their apices; more than 38 postnodal cross-veins and postsubnodal cross-veins; 3-4 rows of cells between Costa and RA distal of pterostigma; three rows of cells between RA and RP1 and between RP1 and IR1.

Specimen MM 1255. Distal four fifth of a wing, dark brown, very similar to the two other specimens, fragment 40 mm long, 12.3 mm wide, main differences with the two other specimens are as follows: wing narrower; cubito-anal area narrower; distance between nodus and base of IR2 longer; only one row of cells between RA and RP1 below pterostigma.

Discussion. These fossils, although only partly preserved, can be attributed to the same species because they have the same wing coloration, size and general pattern of venation. The only potential difference between the holotype and In.37782 is the lack of the distal antenodal crossveins of the second row in the former, but this is probably due to a taphonomic bias. The differences between the holotype and MM 1255 are attributable to fore- and hindwing differences. The hindwings are generally broader with a broader cubito-anal area in these damselflies.

This species has several of the main diagnostic characters of the genus *Labandeiraia* n. gen., i.e. numerous antenodal cross-veins of first and second rows discoidal cell elongate and narrow; anal area very broad and crossed by very long and narrow transverse cells; cubito-anal area very broad and with six long secondary longitudinal veins (three convex and three concave); more than two rows of cells between C and RA distal of pterostigma and between RA and RP1 below it; no pterostigmal brace; at least two long secondary longitudinal veins between all main veins. The available characters exclude affinities with the other known Epallagidae. The most important difference with *Labandeiraia americaborealis* n. sp. is the absence of basal curving of RP1/2. Its only unknown important structures concern the primary antenodal cross-veins and their rela-

tive position to the arculus. Thus we include it in the genus *Labandeiraia* n. gen.

GENUS: *Litheuphaea* Fraser 1955

Type species: *Litheuphaea carpenteri* Fraser 1955. Other species. *L. ludwigi* Bechly 1998, and *Litheuphaea coloradensis* n. sp.

Litheuphaea coloradensis n. sp.

Plate 4

Material. Holotype PI II 562, A.J.E. Presd coll., British Museum of Natural History, London, UK.

Etymology. After the Colorado state.

Age and Outcrop. Eocene, Green River Formation, Douglas Pass, Radar Dome, Garfield County, Colorado, USA.

Diagnosis. *L. coloradensis* n. sp. differs from *L. carpenteri* in the following points: pterostigma covering only six cells instead of 14; subdiscoidal space free of cells, instead of being crossed by two veinlets; cubito-anal area with seven rows of cells instead of 10 in its widest part; only 10 secondary antenodals instead of 19; discoidal cell apparently crossed by a veinlet; 23 postnodals instead of more than 43; only one cell between the origins of RP3/4 and IR2; basal side of pterostigma less oblique, with no cross-vein between it and costal margin. Differences from *L. ludwigi* are less numerous, only its arculus is closer to Ax2 than to Ax1, and cubito-anal area broader.

Description. Print of a nearly complete wing, with only nodal region partly broken, wing 25.9 mm long, 7.7 mm wide, very broad and divided into numerous small cells; distance from base to arculus 2.3 mm, from arculus to nodus 6.7 mm, from nodus to pterostigma 11.4 mm, from pterostigma to wing apex 1.8 mm; pterostigma 3.9 mm long, 0.8 mm wide, covering 13 cells disposed in 2-3 rows, basal side of pterostigma very oblique, more oblique than distal side, but without cross-vein between it and Costa, pterostigmal brace absent, anal area broad, with few large and narrow transverse cells and three rows of cells in its widest part, 0.4 mm wide in its middle; median area free of cells; submedian area with only CuP; discoidal cell elongate and narrow, 0.3 mm wide; no antefurcal cross-veins between basal parts of RP and MA; primary antenodal cross-veins Ax1 and Ax2 stronger than secondaries, Ax1 1.6 mm from wing base, distance between Ax1 and Ax2 0.86 mm; 10 secondaries of first row between Ax2 and nodus; no secondaries of the second row; arculus only slightly basal of Ax2; kink of ScP at nodus very abrupt and Z-like; subnodus aligned with nodal cross-vein Cr; base of RP3/4 distinctly closer to arculus than to nodus, base of IR2 one cell, 0.6 mm distally; basal curving of RP1/2; seven cross-veins in antesubnodal area; postdiscoidal area with only one row of cells between discoidal cell and nodus level, but greatly widened distally,

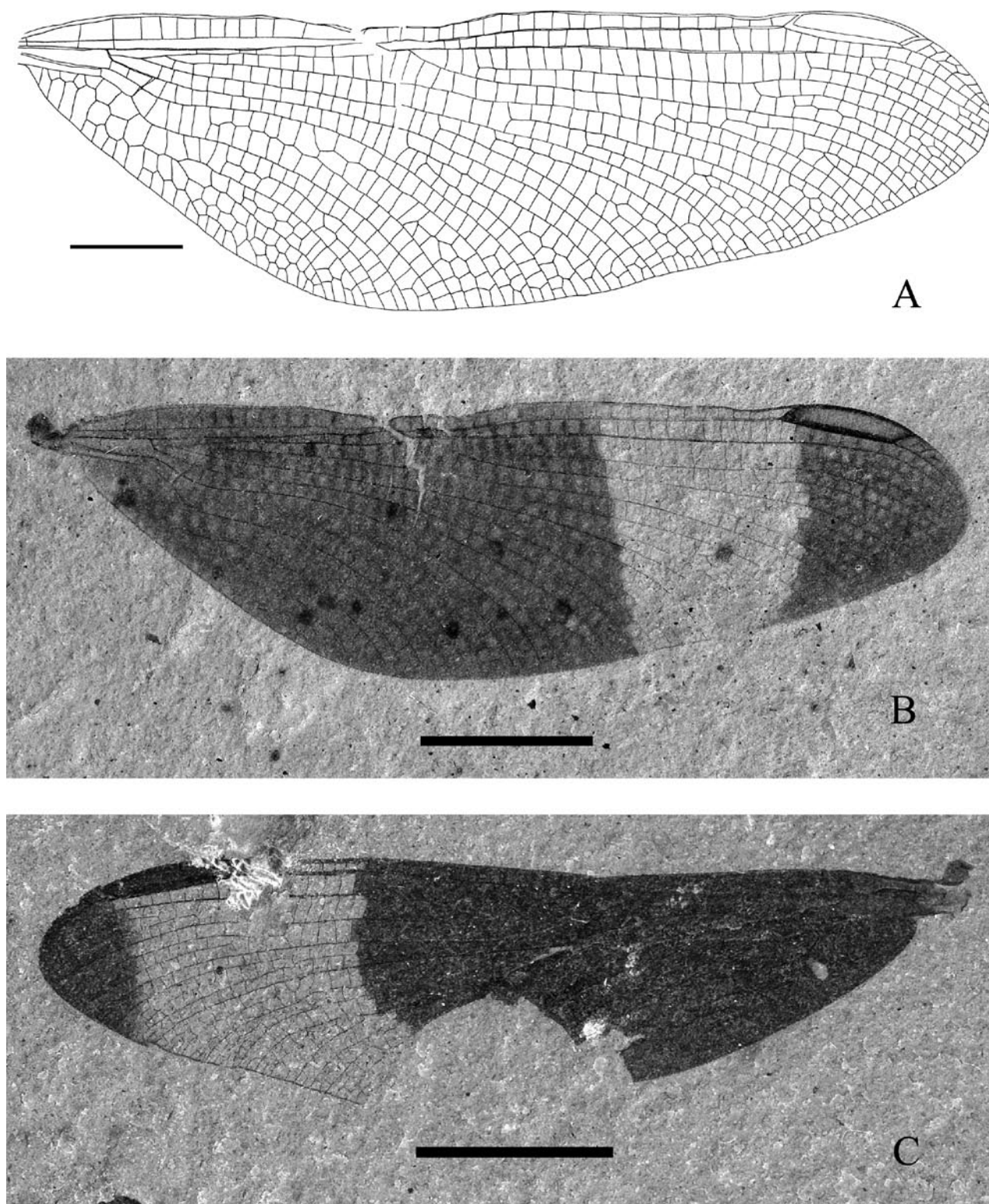


Plate 4. *Litheuphaea coloradensis* n. sp., holotype PI II 562. A, drawing of wing (scale bar represents 3 mm). B, part, photograph. C, counterpart, photograph (scale bars represent 5 mm).

and with two long secondary longitudinal veins; area between MP and CuA progressively broadened and with two long secondary longitudinal veins; CuA not forked; cubito-anal area very broad, 2.6 mm wide in its broadest part, and with one long concave secondary longitudinal vein; area between MA and RP3/4 narrow between arculus and nodus; area between RP3/4 and IR2 progressively broadened, with two long secondary longitudinal veins; base of RP2 one cell distal of subnodus; base of IR1 close to that of RP2; IR1, RP2, IR2, and RP3/4 rather straight and faintly curved near their apices; 23 postnodal cross-veins and numerous post-subnodal cross-veins; 1-2 rows of cells between Costa and RA distal of pterostigma; one row of cells between RA and RP1; 2-3 rows of cells between RP1 and IR1.

Discussion. This fossil has all the diagnostic characters of the genus *Litheuphaea*, as listed by Bechly (1998: 36). It is more similar to *L. ludwigi* than to *L. carpenteri*, especially in its less dense wing venation.

BIOGEOGRAPHY

In a molecular phylogenetic analysis of Caloptera, Dumont *et al.* (2005) proposed the Chlorocyphidae as sister group of the Epallagidae, and the Amphipterygidae as sister group of the Polythoridae (+ Dicteriadidae), all five groups being in basal position relative to the Calopterygidae. This analysis did not comprise fossil taxa and neglected some calopteran families. The phylogenetic analysis of Bechly (1996) is also of interest to study the biogeographic history of this group as it includes the recent and fossil taxa.

Bechly (1996) proposed the Polythoridae to be the sister group of the Epallagoidea. Recent Polythoridae are endemic to the Neotropical region and the Epallagoidea include the families Zacallitidae and Epallagidae. The Zacallitidae is a fossil group only known so far from the Eocene of Colorado (Cockerell 1928). The Epallagidae comprises the Eodichrominae and the Epallaginae. The Eodichrominae comprise four genera from the Paleogene, namely the North American *Eodichroma*, the Western European *Parazacallites*, *Litheuphaea* from Baltic amber and North America, and *Labandeiraia* n. gen. from Denmark and North America. A similar distribution can be found in the Paleogene damselfly group Thaumtoneuridae: Dysagrioininae Cockerell (1908), the dragonfly genus *Oligaeschna* Piton & Théobald 1939, and in the neuropteran Polystoechotidae (Nel *et al.* 1994, 2005, Nel & Arillo 2006, Archibald & Makarkin 2006).

Two other families of Euloptera belonging to the clades Calopterygomorpha Bechly (1996) and Amphipterygida Bechly (1996) are newly discovered in the fossil record. That is the case of the Bolcathoridae Gentilini (2002) from the Early Eocene of Monte Bolca (Italy) (Papazoni & Trevisani 2005, Trevisani *et al.* 2005), which is closely related to the Polythoridae (Gentilini 2002); the amphipterygid Baltic amber genus *Pamita* (May & Carle 2005), and the amphipterygoid Latibasaliidae Petrulevičius & Nel (2004) from the late Paleocene of Maíz Gordo, Northwest

Argentina (Petrulevičius & Nel 2004). The Bolcathoridae have been also recently discovered in the Early Oligocene of the Isle of Wight (UK) (Nel unpublished).

The fossil record of the Chlorocyphidae and Dicteriadidae remains very scarce (Nel & Paicheler 1992). Nevertheless, both epallagoid and polythorid clades were present in the warm 'tropical' Paleogene Europe, North and probably South America. The direct contact between North America and Europe during the Paleogene was not obvious as the Northern Atlantic Ocean was nearly opened at that time. Nevertheless, there are several geological investigations that support the fact that a series of land connections existed in the Eocene (Scotese 1997, Knox 1998), and similar distributional patterns as for the Odonata are also known for Paleogene mammals (e.g. McKenna 1975, Hooker & Dashzeveg 2003) and plants (e.g. Tiffney 1985, Davis *et al.* 2002, Pennington & Dick 2004, Milne 2006). Some authors explain such patterns by trans-Beringian contacts (e.g. Beard & Dawson 1999), but recent analyses of animal dispersal, vicariance, and diversification in the Holarctic mainly with insects but also with other invertebrates and vertebrates show that trans-Atlantic distributions were common in the Late Cretaceous to Mid Tertiary (70-20 Ma), whereas trans-Beringian distributions were rare in that period (Sanmartín *et al.* 2001). Another solution to explain the Paleogene distribution of the Epallagidae would be their possible great antiquity in the Cretaceous, as the amphipterygid family Thaumtoneuridae is recorded from the Early Cretaceous (Bechly 1996). Fossil representatives of the sister group of Amphipterygida, the Calopterygomorpha are still unknown in the Cretaceous. We have to take into account the presence of the Amphipterygida family Latibasaliidae in South America. Its presence in the late Paleocene gives a wider known distribution of the Euloptera in the early Paleogene. This record suggests an interchange of such animals between South America and North America during the Cretaceous and the lower Tertiary; these interchanges are also recorded by terrestrial vertebrates during the Palaeocene (Rage 1996).

Remarks. Other fossil taxa that have been attributed to the Polythoridae are *incertae sedis* (Nel & Paicheler 1992, Bechly 1996). Also the Green River Eocene genus *Protamphipteryx* Cockerell 1920, is very poorly described and figured and would need a complete revision (Cockerell 1920: 236, pl. 32, fig. 3) for its accurate attribution to the Amphipterygidae.

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