[Palaeontology, Vol. 51, Part 3, 2008, pp. 709–713]

THE FIRST DAMSELFLIES FROM THE LOWERMOST EOCENE OF DENMARK, WITH A DESCRIPTION OF A NEW SUBFAMILY (ODONATA, ZYGOPTERA: DYSAGRIONIDAE)

by JES RUST*, JULIAN F. PETRULEVIČIUS† *and* ANDRÉ NEL‡

*Institute of Palaeontology, University of Bonn, Nussallee 8, 53115 Bonn, Germany; e-mail: jrust@uni-bonn.de
†Div. Cient. Paleozoología Invertebrados, Museo de La Plata, Fac. Cs. Nat., UNLP and CONICET Argentina; e-mail: levicius@museo.fcnym.unlp.edu.ar
‡CNRS UMR 5202, CP 50, Entomologie, Muséum National d'Histoire Naturelle, Paris, France, e-mail: anel@mnhn.fr (corresponding author)

Typescript received 3 January 2007; accepted in revised form 25 June 2007

Abstract: *Eodysagrion mikkelseni* gen. et sp. nov., type species of the new subfamily Eodysagrioninae, and the dysagrionine *Primorilestes madseni* sp. nov., the first thaumatoneurid damselflies from the lowermost Eocene of Denmark, are described. They confirm the presence of this American family in the Palaeogene of Western Europe.

Key words: Insecta, Odonata, Zygoptera, Dysagrionidae, Eodysagrioninae, new genus, new species, Eocene, Denmark.

AMPHIPTERYGIDA are rather scarce in the fossil record. The oldest representatives are the Early Cretaceous *Euarchistigma* Carle and Wighton, 1990 and the Late Jurassic *Congqingia* Zhang, 1992 (Bechly 1996). In the Cenozoic, this clade is represented by two amphipterygid genera and the extinct groups Dysagrioninae Cockerell, 1908 (five early Cenozoic genera) and the monogeneric Latibasaliidae Petrulevičius and Nel, 2004 (Petrulevičius and Nel 2004; May and Carle 2005; Nel and Arillo 2006). Therefore, the description here of a new subfamily and two new species of 'thaumatoneurids' from the lowermost Eocene of Denmark is of great interest for understanding the past diversity of this clade. The only Recent Dysagrionidae: Thaumatoneurinae (see below) is the Neotropical *Thaumatoneura inopinata* McLachlan, 1897. Several Cenozoic representatives of this family have been found in the Palaeogene of North America, Siberia and Europe, congruent with the present discoveries. *Thaumatoneura* McLachlan, 1897 appears to be a relic of an ancient and fairly diverse group during the Cenozoic. The extinction of the North American and European 'thaumatoneurids' can be explained by the climatic degradations of the Miocene and Plio-Pleistocene. However the absence of any Recent representative of this family in the warm, humid forests of South-East Asia remains unexplained since the Old World lineages of this group presumably had the opportunity to migrate south.

We follow the wing venation nomenclature of Riek and 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 herein are based on the phylogenetic system of Bechly (1996).

SYSTEMATIC PALAEONTOLOGY

Clade AMPHIPTERYGIDA Bechly, 1996
Family DYSAGRIONIDAE Cockerell, 1908

Remarks. Tillyard and Fraser (1938) erected the subfamily Thaumatoneurinae and Fraser (1957) implied that *Dysagrion* belonged there. Bechly (1996) elevated Thaumatoneuridae to family status with the two subfamilies Thaumatoneurinae and Dysagrioninae. However, Cockerell (1908) had already recognized the Dysagrioninae, so this name has priority over Thaumatoneurinae; hence, the correct name for the family-level taxon containing *Dysagrion* and *Thaumatoneura* is Dysagrionidae, with Thaumatoneurinae available as subfamily name within it.

Subfamily EODYSAGRIONINAE subfam. nov.

Type genus. Eodysagrion gen. nov.

Diagnosis. Wing characters only. Petiole short; antenodal area broadened at level of the two primary antenodal crossveins; discoidal cell rectangular with distal side

 doi: 10.1111/j.1475-4983.2008.00780.x

directed towards wing base; no oblique vein O; no secondary antenodal crossveins; antesubnodal space free; bases of IR2 and RP3/4 opposite or close to subnodus; IR2 apparently arising on RP3/4; nodus in basal position, but only 30 per cent of wing length; longitudinal wing veins not distally distinctly curved to the posterior wing margin; postdiscoidal crossveins relatively few.

Genus EODYSAGRION gen. nov.

Type species. Eodysagrion mikkelseni sp. nov.

Derivation of name. After the Eocene Epoch and the genus *Dysagrion*.

Diagnosis. As for the subfamily.

Eodysagrion mikkelseni sp. nov.
Text-figure 1

Derivation of name. After the collector B. S. Mikkelsen.

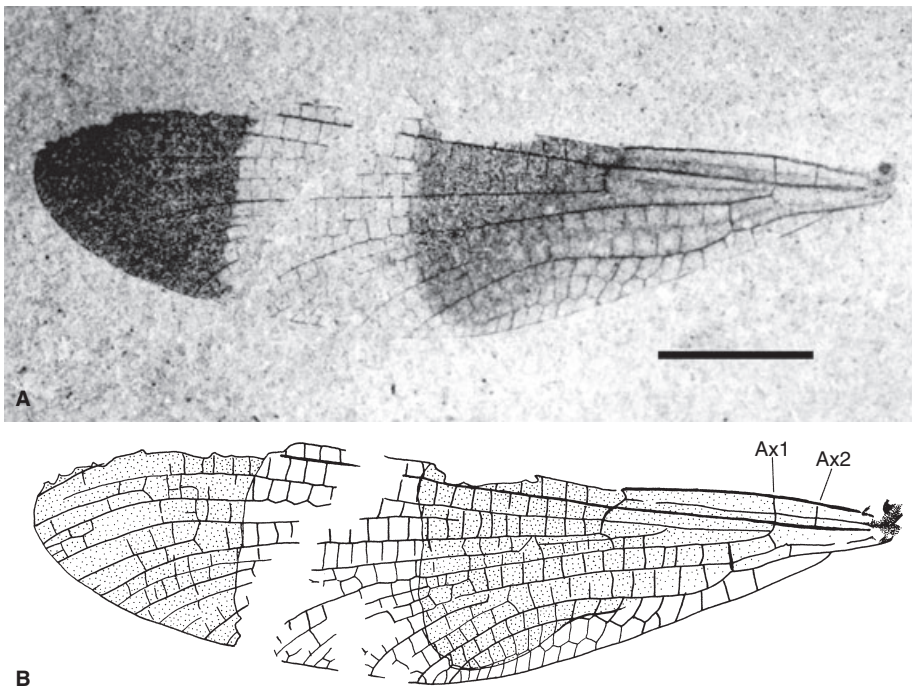
Material. Holotype MM I842a–b, coll. B. S. Mikkelsen, Molermuseum, Mors, Denmark. Only known specimen.

Occurrence and age. Fur Formation ('Mo clay'), diatomite, Denmark; earliest Eocene.

Diagnosis. As for the subfamily. A hyaline area crosses wing basal of pterostigma and two darker areas in basal two-thirds of wing and at wing apex.

Description. A nearly complete wing with the costodistal margin missing, basal half brown; a hyaline area crosses it and is very dark at apex, 25.0 mm long, 6.3 mm wide; distance from base to arculus 3.0 mm, from arculus to nodus 4.4 mm, from nodus to apex 1.7 mm; petiole 1.5 mm long, 1.3 mm wide; distance from base to A × 1 2.0 mm, from A × 1 to A × 2 1.0 mm; A× 2 aligned with arculus; no secondary antenodal crossvein; antesubnodal space free; median space free; submedian space crossed by CuP; discoidal cell rectangular-elongate, 1.4 mm long, 0.5 mm wide; base of RP3/4 close to subnodus, 1.6 mm basal; base of IR2 below subnodus; base of RP2 six cells, 4.0 mm distal of subnodus; base of IR1 about three cells distally; IR1 basally zigzagged, one secondary longitudinal vein between IR1 and RP1, none between IR1 and RP2, one between RP2 and IR2, two between IR2 and RP3/4, two between RP3/4 and MA, two between MA and MP, two between MP and CuA, one in cubitoanal area, three rows of cells in same area; CuA curved but other veins nearly straight.

Discussion. The rectangular discoidal cell with its distal side directed towards the wing base, perpendicular to its anterior side, strong, and aligned with the basal part of CuA supports the referral to the Eucaloptera. Affinities with the Sieblosiidae can be excluded because of the absence of oblique vein O, a base of IR2 below the sub-



TEXT-FIG. 1. *Eodysagrion mikkelseni* gen. et sp. nov., holotype MM I842a–b. A, photograph, and B, interpretative drawing of wing; scale bar represents 4 mm.

nodus, and the distal side of the discoidal cell not longer than the basal side. Within the Eucaloptera, the absence of secondary antenodal crossveins between ScP and RA and the free antesubnodal space supports a referral to the clade Amphipterygida. The two families Diphlebiidae and Pseudolestidae can be excluded because of bases of IR2 and RP3/4, which are opposite or close to the subnodus. The nodus in a basal position, at 30 per cent of the wing length, supports referral to Amphipterygoidea. The Amphipterygidae have secondary antenodal crossveins between C and ScP and the bases of RP3/4 and IR2 are closer to the arculus than to the subnodus, unlike *Eodysagrion* gen. nov. The fossil family Latibasaliidae has no secondary antenodal crossveins, as in *Eodysagrion*, but the bases of RP3/4 and IR2 are closer to the arculus than to the subnodus. The only other family is the Dysagrionidae, in which the base of IR2 is opposite the subnodus and that of RP3/4 close to it, and which in some taxa have no secondary antenodal crossveins. Bechly (1996) proposed as synapomorphies of this last family the antesubnodal space without any crossveins (also present in Latibasalidae), and the basal costal margin between the wing base and nodus distinctly curved convexly. This character could be more correctly expressed as follows: antenodal area broadened at the level of the two primary antenodal crossveins. It is present in *Eodysagrion*, although rather weakly indicated. Within this group, *Eodysagrion* shares two apomorphies with the Thaumatoneurinae: 'discoidal cell perfectly rectangular' and 'IR2 apparently arising on RP3/4'. However, *Eodysagrion* differs markedly from the two thaumatoneurine genera *Euarchistigma* Carle and Wighton, 1990 and *Thaumatoneura* in its clearly less numerous secondary longitudinal veins, its nodus not in a very basal position, less numerous postdiscoidal crossveins, and its longitudinal wing veins not distinctly curved distal to the posterior wing margin. *Eodysagrion* cannot be considered to belong to the Dysagrioninae because its discoidal cell is not of the 'sieblosiid' type, i.e. with a distal side distinctly longer than its basal side and anterior and posterior sides not parallel (Bechly 1996; Nel *et al.* 2005; Nel and Arillo 2006). Except for this character, its wing venation is very similar to that of the dysagrionine genus *Primorilestes* Nel, Petrulevičius and Jarzembowski, 2005.

There are three states of evolution of the discoidal cell in the Amphipterygidae-Thaumatoneuridae: (1) the plesiomorphic amphipterygid type with the anterior and posterior sides parallel, but the basal and distal sides not parallel; (2) the thaumatoneurine state with a rectangular discoidal cell; (3) the 'sieblosiid-dysagrionine' type. Two patterns of evolution are possible: the first state gives rise to the second and the second gives rise to the third, or the first state gives rise to the second and third states. The first implies that *Eodysagrion* is a dysagrionid but not a thaumatoneurine because it lacks apomorphies of this subfamily that do not concern the discoidal cell. It would belong to the dysagrionine lineage, but as a potential sister group of the subfamily. The second implies that *Eodysagrion* belongs to the thaumatoneurine lineage, but as the potential sister group of this subfamily.

In summary, the exact position of *Eodysagrion* within the Dysagrionidae is uncertain. We consider that it represent a new genus and subfamily, distinct from both Dysagrioninae and Thaumatoneurinae.

Subfamily DYSAGRIONINAE Cockerell, 1908

Genus PRIMORILESTES Nel, Petrulevičius and Jarzembowski, 2005

Type species. Primorilestes violetae Nel, Petrulevičius and Jarzembowski, 2005.

Primorilestes madseni sp. nov.
Text-figure 2

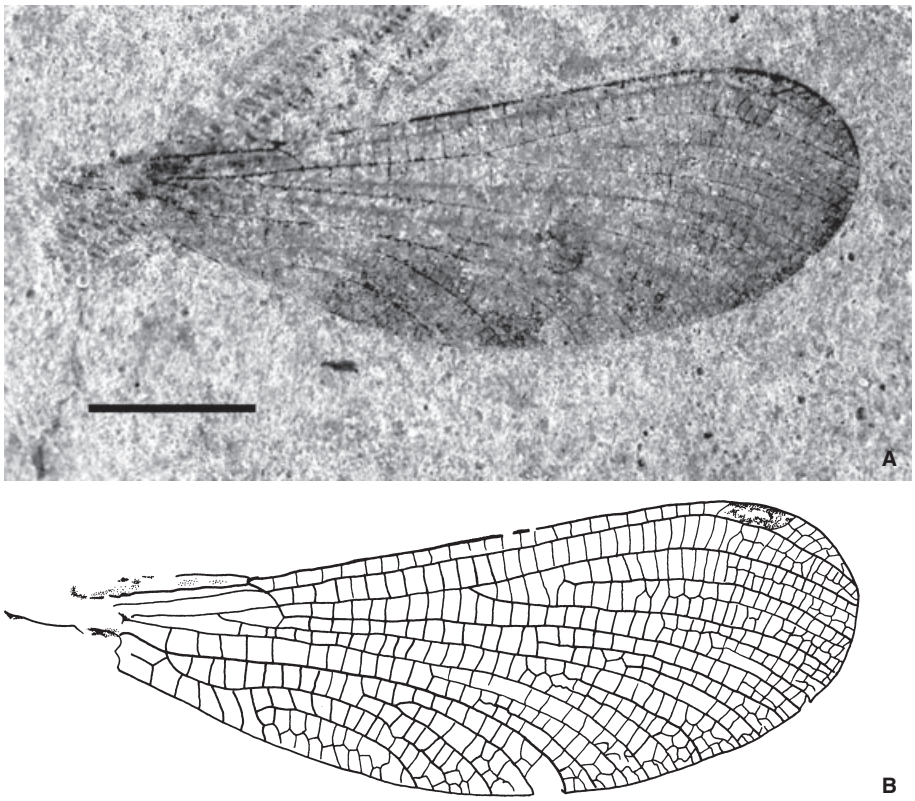
Derivation of name. After the collector H. Madsen.

Material. Holotype MM 14M–A2786a–b, collection H. Madsen, Molermuseum, Mors, Denmark. Only known specimen.

Occurrence and age. Fur Formation ('Mo clay'), diatomite, Denmark; earliest Eocene.

Diagnosis. Wing characters only. Cubito-anal area with three rows of cells; base of RP2 11 cells distal of subnodus; two rows of cells between C and RA and between RA and RP1 distal of pterostigma.

Description. A nearly complete wing, with the extreme base missing; wing dark brown, *c.* 23.0 mm long, 7.3 mm wide; distance from base to arculus *c.* 3.2 mm, from arculus to nodus 3.6 mm, from nodus to pterostigma 12.8 mm; pterostigma 2.2 mm long, 5.8 mm wide, without strong pterostigmal brace; distance between pterostigma and wing apex 2.9 mm; length of petiole unknown, but probably short; A × 1 and A × 2 not preserved; no secondary antenodal crossvein; antesubnodal space free; median space free; submedian space crossed by CuP; discoidal cell rectangular and elongate, 1.1 mm long, 0.7 mm wide, with its basal side distinctly shorter than the distal side; base of RP3/4 close to subnodus, 1.6 mm basal; base of IR2 below subnodus; base of RP2 11 cells, 5.1 mm distal of subnodus; base of IR1 about five cells distally; IR1 not zigzagged, two rows of cells between C and RA and between RA and RP1 distal of pterostigma; one secondary longitudinal vein between IR1 and RP1 and between IR1 and RP2, two between RP2 and IR2, two between IR2 and RP3/4, two between RP3/4 and MA, two



TEXT-FIG. 2. *Primorilestes madseni* sp. nov., holotype MM 14M–A2786a–b. A, photograph, and B, interpretative drawing of wing; scale bar represents 4 mm.

between MA and MP, two between MP and CuA, one in cubito-anal area, three rows of cells in the same area; MP and CuA curved.

Discussion. This wing is very similar to those of the North American *Dysagrion* Scudder, 1878 and the East Siberian *Primorilestes*, especially in the shape of the discoidal cell, probable short petiole, broad cubito-anal area, curved CuA, bases of RP3/4 and IR2, no oblique vein O, and base of RP2 in a very distal position. Its referal to Dysagrioninae is based on its discoidal cell of a 'sieblosiid-dysagrionine' type, with its distal side longer than its basal side and anterior and posterior sides not parallel. *Primorilestes madseni* sp. nov. differs from the Dysagrionini Cockerell, 1908 in the absence of secondary antenodal crossveins distal of A × 2 (Nel and Arillo 2006); the same character would support affinities with the Petrolestini Cockerell, 1927 and *Primorilestes*. It differs from the two petrolestine genera *Petrolestes* Cockerell, 1927 and *Congqingia* Zhang, 1992 in having its base of IR2 distinctly basal of the subnodus (Zhang 1992; Nel and Paicheler 1994).

Visible differences compared to *Primorilestes violetae* are as follows: cubito-anal area narrower with three rows of cells instead of six in *P. violetae*; base of RP2 11 cells distal of subnodus instead of six. These differences only merit species status.

Acknowledgements. We thank H. Madsen and B. S. Mikkelsen for their kind help and authorization to study the type material. We also acknowledge two anonymous referees for improving the manuscript with their very useful comments.

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