International Journal of Odonatology 1 (1): 33-63, 1998.

NEW FOSSIL DAMSELFLIES FROM BALTIC AMBER, WITH DESCRIPTION OF A NEW SPECIES, A REDESCRIPTION OF *LITHEUPHAEA CARPENTERI* FRASER, AND A DISCUSSION ON THE PHYLOGENY OF EPALLAGIDAE (ZYGOPTERA: CALOPTERA)

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Received 23 June 1998; accepted 29 June 1998

Abstract

Litheuphaea ludwigi sp. n. is described as first representative of Epallagidae from Baltic amber. The holotype of *Litheuphaea carpenteri* Fraser, 1955 is redescribed, the phylogenetic position of all fossil Epallagidae is discussed, and a new phylogenetic classification is proposed. The authorship of Selys (1853) for the family-group name Euphaeidae is rejected, since the "légion Euphaea" proposed by Selys is neither a noun in the nominative plural, nor ending in a latinized suffix. Consequently, the correct family name must be Epallagidae Needham, 1903, since Euphaeidae were first established by Jacobson & Bianchi (1905) and thus have to be considered as a junior subjective synonym. Similarly, all the other "légions" proposed by Selys are rejected as available family-group taxa, so that the next available family-group name has to be used, e.g. Heliocharitidae Tillyard & Fraser, 1939 instead of Dicteriadidae Montgomery, 1959 (nec Selys, 1853). Parazacallitinae Nel, 1988 is considered as junior subjective synonym of Eodichromatinae Cockerell, 1923 which is regarded as an extinct subfamily of Epallagidae, comprising the sister-tribes Litheuphaeini Bechly, 1996 and Eodichromatini stat. nov. for the sister-genera *Eodichroma* Cockerell, 1923 and *Parazacallites* Nel, 1988. Zacallitidae Cockerell, 1928 is restored as a distinct family and preliminarily regarded as the sister-group of Epallagidae. A unique fossil odonate is briefly described, which represents a damselfly in Baltic amber that is just emerging from the exuvia (probably Platystictidae or Megapodagrionidae). An annotated new catalogue of all known odonates in amber is provided, including 46 specimens from Lebanon, Dominican, Baltic and Saxonian amber, of which 3 specimens are adult Anisoptera and 5 specimens are exuviae. A lectotype for *Platycnemis? antiqua* (Pictet & Hagen, 1856) is designated and illustrated.

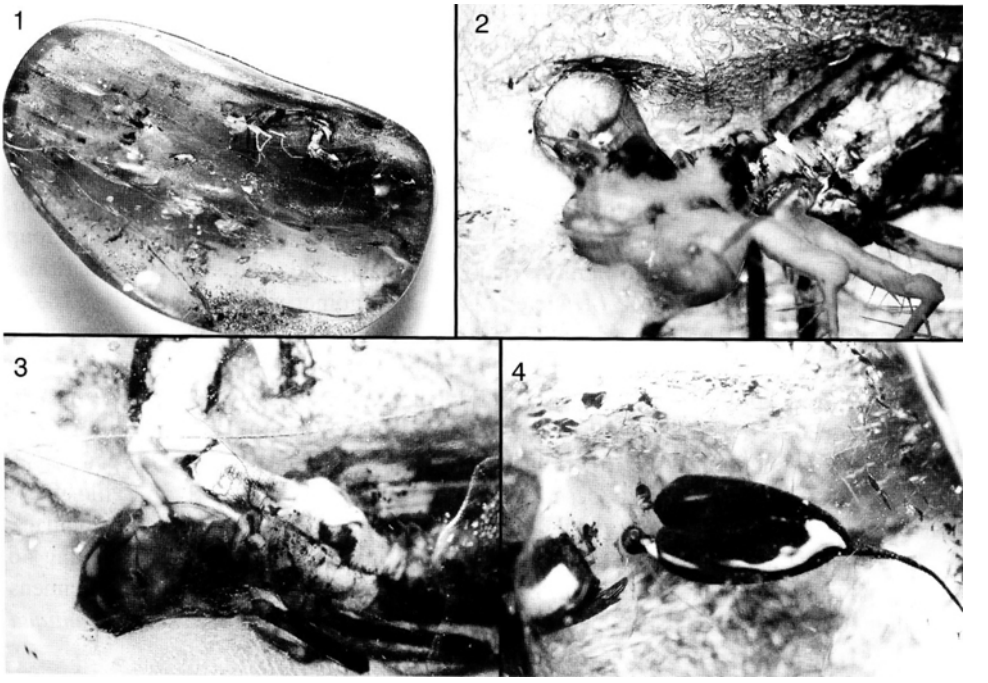
Introduction

Dragonflies and damselflies certainly represent the most spectacular insect inclusions in Tertiary amber, but are also among the rarest. Only one fragmentary odonate is yet known from Mesozoic amber (see below). Because of this rarity dragonflies are not even mentioned in a recent book on insects in amber (Krzeminska & Krzeminski, 1992).

Bechly (1993, 1996b) reviewed the then known amber dragonflies and could document only 32 specimens from Dominican and Baltic amber. An updated and revised catalogue of all known odonates (46 specimens) in amber is provided below.

Larsson (1978: 82-83) discussed the presence of odonate adults and larvae or exuviae in Baltic amber. Most odonates preserved in amber are damselflies due to the conditions of fossilisation: small damselflies (Zygoptera) are more easily trapped and enclosed in resin than the larger dragonflies (Anisoptera). Furthermore, they hover in dense vegetation and therefore are more likely to contact resin than dragonflies, which mostly patrol open areas. Consequently, Anisoptera preserved in amber are extremely rare (only three specimens yet known) and thus rather precious fossils (Orr, 1993).

Recently I studied four amber damselflies in the outstanding private amber collection of Mr Walter Ludwig (Berlin, Germany). Among these specimens are the first two odonates from Saxonian amber of Bitterfeld (see below; figure 12). The other two specimens are from Baltic amber (Palmnicken) and of particular scientific importance. The first specimen is a female damselfly embedded during emergence, with the apex of the abdomen still concealed in the exuvia, which is also completely preserved (figures 1-4).



Figs 1-4: Emerging damselfly in Baltic amber, specimen [without number] in coll. W. Ludwig, Berlin: (1) piece of amber (max. length, 57.4 mm); - (2) head of the emerging damselfly; - (3) head and thorax of the exuvia, with a part of the emerging abdomen; - (4) saccoid caudal gills with terminal filamentous projection, and ovipositor of the exuvia.

This exuvia (total length with gills, 11 + 6 mm) is most interesting since it has a well-developed ovipositor and saccoid caudal gills with long terminal filaments. This type of

gill is only known from some extant tropical damselflies, like Polythoridae, Epallagidae, Diphlebiidae, Platystictidae-Palaemnematinae and some Megapodagrionidae (e.g. *Hypolestes*, *Heteragrion* and *Oxystigma*). Unfortunately the wings of the specimen were not yet unfolded, so that the wing venation is completely invisible. Since the larva does not have lateral abdominal gills it cannot belong to Polythoridae or Epallagidae, but most likely belongs to Platystictidae or Megapodagrionidae. The presence of so-called "clouded white substance" around parts of the damselfly remains clearly excludes a forgery.

The second specimen described in detail below, represents the first calopterygoid damselfly (higher taxon Caloptera *sensu* Bechly, 1996a) and the first Epallagidae preserved in amber. This amber specimen is closely related to *Litheuphaea carpenteri* Fraser, 1955 from a Middle Oligocene mudstone of Oregon. However, this relationship became evident only after re-examining the holotype of the latter species, because the original description contained several substantial errors. Therefore a redescription of this holotype is also provided below.

Material and methods

The presented results are based on my examination of the fossil and amber collections at SMNS (Stuttgart), BSPGM (Munich), MNHB (Berlin), coll. Ludwig (Berlin), and MCZ (Cambridge), as well as on a review of all available literature. All drawings were made with camera lucida, and all photos were made with a SLR camera and macro lens.

In the following study I have adopted the wing venation nomenclature of Riek (1976) and Riek & Kukalová-Peck (1984), amended by Kukalová-Peck (1991), Nel et al. (1993) and Bechly (1996a). The proposed phylogenetic classification of Zygoptera was introduced by Bechly (1996a), amended by Bechly (1997) and is strictly based on the principles of consequent phylogenetic systematics (*sensu* Hennig, 1966, 1981), rather than so-called "numerical cladistics" (for reasons see Wägele, 1994; Borucki, 1996; and Bechly, 1997). Therefore the characters were not analysed with a computer parsimony software (e.g. Paup) , but by "hand" (rather by brain), based on a more global concept of parsimony that includes a priori weighting according to the different compatibility and complexity of the characters. Alleged non-weighting of characters is a myth, since the selection and delimitation of the characters represent a strong, though often unconscious, weighting procedure. Non-weighting therefore indeed represents equal weighting, and has to be regarded as unrealistic, since the case that all characters have the same weight (meaning the same truth-probability of the referring homology hypothesis) is most unlikely.

All recognized monophyla have been named, since the sequencing of stem-group representatives has to be rejected because of the logical and practical reasons described by Willmann (1989). The popular criticism that this leads to an inflation of names, is rather unconvincing regarding the many million species that still have to be described. Why should all of them be named, but not all monophyla? Monophyla are natural entities that deserve a proper name, and often are more important than many species taxa (e.g. all odonatologists will of course know the taxon Aeshnidae, but how many ever heard of *Oreaeschna dominatrix*?). Redundant taxa and the assignment of formal categorial ranks

have been omitted whenever possible without violation of the International Rules of Zoological Nomenclature (IRZN), because they are arbitrary and superfluous (Willmann, 1989). As recently suggested by Cantino et al. (1997), for each proposed taxon a phylogenetic definition, a list of the referring autapomorphies (the synapomorphies of its members) and a list of the currently known members of the taxon is provided according to "phylogenetic taxonomy" after De Queiroz & Gauthier (1990, 1992). This taxonomical approach is not dependent on the view of taxa as "individuals" (of logic), since it implies definitions of names rather than groups, so that this approach is equally useful and even more preferable if taxa are understood as concepts ("logical classes", or "natural kinds" *sensu* Mahner & Bunge, 1997).

Short sketch of the phylogenetic system of Zygoptera of Bechly (1996a, 1997): Zygoptera are monophyletic and comprise the sister-groups Caloptera (= Calopterygoidea auct.) and Euzygoptera. Euzygoptera comprises the sister-groups Lestomorpha (= Hemiphlebioidea auct. + Lestinoidea auct.) and Coenagrionomorpha (= Coenagrionoidea auct.). Caloptera comprises the fossil stem-group of extant Caloptera (Eucaloptera), and the crown-group sister-taxa Amphipterygida (including Diphlebiidae, Pseudolestidae, Thaumatoneuridae, and Amphipterygidae) and Calopterygomorpha. The latter taxon comprises the sister-groups Chlorocyphoidea (= Chlorocyphidae auct.) and Calopterygiformia. Calopterygiformia comprises the sister-groups Euphaeida (see below) and Calopterygida (Heliocharitidae and Caliphaeidae + Calopterygidae). Detailed information about this new phylogenetic system, including lists of the referring synapomorphies, is also available on the Internet at http://members.aol.com/odonatadat/phylogeny/bechly.htm.

Systematic paleontology

Genus *Litheuphaea* Fraser, 1955

Type-species. – *Litheuphaea carpenteri* Fraser, 1955.
Other species. – *Litheuphaea ludwigi* sp. n.

New differential diagnosis. – Wing venation similar to recent Epallagidae, but with a longer pterostigma, and a more basal position of the nodus. Further significant distinctions from all recent Epallagidae are the enlarged cubito-anal area with a unique accessory concave "anal" vein (synapomorphy with Eodichromatinae); the approximation of Ax1 and Ax2 (synapomorphy with Eodichromatinae); the absence of antefurcal crossveins between the basal parts of RP and MA (synapomorphy with Eodichromatinae). Significant distinctions from the other two genera of Eodichromatinae (*Eodichroma* and *Parazacallites*) are the larger size (probably a plesiomorphy), and the suppression of all secondary antenodals between ScP and RA (autapomorphy; convergent to Amphipterygida *sensu* Bechly, 1996a).

Systematic position. – According to Bechly (1996a, 1997) this genus belongs to Epallagidae - Eodichromatinae within the calopterygoid Zygoptera (clade Caloptera - Calopterygiformia) (also see Discussion below).

Litheuphaea ludwigi sp. n.
Figures 5-8

Material. – Holotype: Specimen without number in the private collection of Walter Ludwig (Berlin, Germany) who announced the donation of the specimen to a public museum (most probably to the Natural History Museum of Berlin).

Stratum Typicum. – Tertiary, Upper Eocene, Baltic amber.

Locus Typicus. – Palmnicken.

Etymology. – After the collector and owner of the holotype, Walter Ludwig (Berlin, Germany).

Differential diagnosis. – This new species is distinguished from *Litheuphaea carpenteri* by the following characters: Less dense wing venation, with fewer cells and intercalary veins; subdiscoidal cell free or only divided by a single crossvein (divided by two crossveins in *L. carpenteri*); only one cell between origins of IR2 and RP3/4 (four cells in *L. carpenteri*); base of RP1/2 more distinctly curved towards RA (midfork symmetrical in *L. carpenteri*); RP2 not aligned with subnodus, but originating somewhat distal to it (aligned with subnodus in *L. carpenteri*); narrower postdiscoidal, postsubdiscoidal, cubito-anal, and anal areas with fewer cells; arculus rather straight and in a more basal position, close to Ax1 (closer to Ax2 in *L. carpenteri*); subnodal veinlet more oblique than nodal veinlet (less oblique than nodal veinlet in *L. carpenteri*); basal side of pterostigma less oblique and no crossvein between it and costal margin; only five cells beneath the pterostigma (about fifteen cells in *L. carpenteri*); only three cells distal to pterostigma are double (all poststigmal cells are double in *L. carpenteri*).

L. ludwigi sp. n. differs from *Parazacallites aquisextanea* Nel, 1988 in its larger size (wing length about 30 mm instead of only 21.5 mm); position of the arculus close to Ax1, but not aligned with it; absence of any secondary antenodal crossveins between ScP and RA; and its less developed intercalary veins in cubito-anal area.

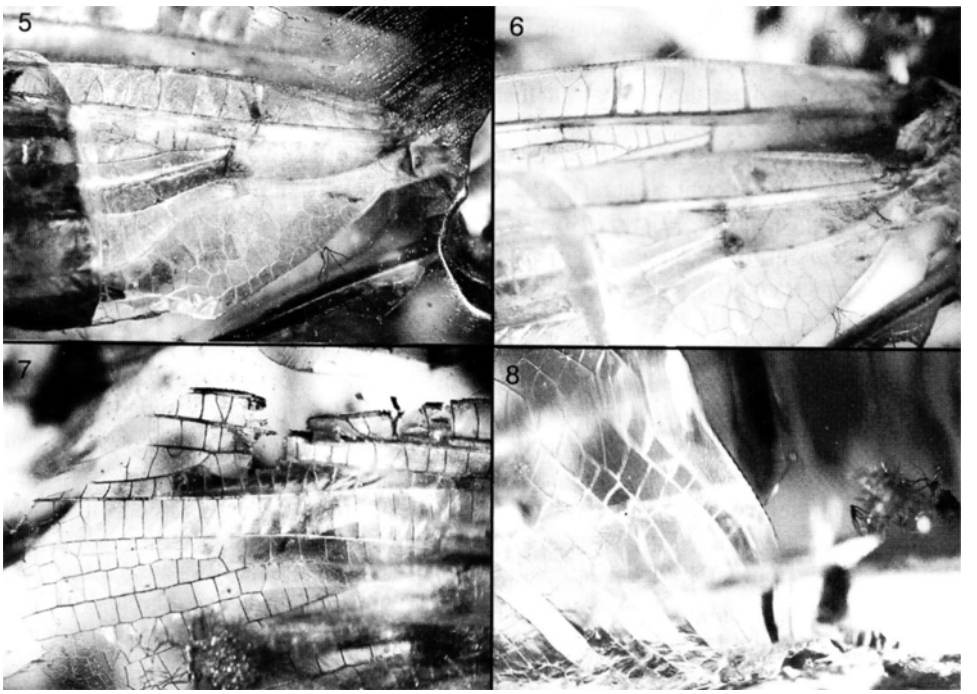
L. ludwigi sp. n. differs from *Eodichroma mirifica* Cockerell, 1923 in its larger size (wing length about 30 mm instead of only 20 mm); absence of typical bicolored wing pattern of *Eodichroma*; absence of unique triadic branching of accessory veins in cubito-anal area; and its more basal position of the nodus.

Description

The holotype is enclosed in a most remarkable piece of amber, which represents a snapshot of the diverse arthropod fauna of the Baltic amber forest. Although of rather small size (max. length, 44 mm; max. width, 21 mm), this piece contains two spiders, two wasps, six flies, three beetles, two cicadas, a caddisfly, and numerous aphids of different instars, and the damselfly fragment described below.

The damselfly remains are represented by a complete left fore wing, the basal half of the right fore wing, and the basal parts of the two hind wings, all connected to a fragment of the pterothorax. The pterothorax is densely haired and has an incomplete interpleural suture. By a unique preservational circumstance, the pterothorax is open to the exterior side of the amber piece, so that a cast of the interior of the pterothorax can easily be made. Even the details of the inner side of the wing articulation are visible. Unfortunately, the

irregular surface of the piece of amber and the distorted and overlapping position of the wings made a drawing of the fossil impossible, and even a satisfying photographic documentation was difficult. Therefore several macro-photos of details (figures 5-8) and a detailed description are provided below.



Figs 5-8: *Litheuphaea ludwigi* sp. n., Baltic amber, holotype specimen [without number] in coll. W. Ludwig, Berlin. [No scales]: (5) basal part of right hind wing; - (6) antenodal area of right fore wing; - (7) middle part of right fore wing; - (8) apex of left fore wing, with pterostigma. Due to the irregular surface of the piece of amber there is a strong optical distortion in this area.

Left fore wing

The wing is bent near the pterostigma and the postnodal area is partly exposed on the surface of the amber piece. Length, about 30 mm; distance from base to arculus, about 3.3 mm; distance from base to midfork, about 4.8 mm; distance from base to nodus, about 11.6 mm (nodus in a relatively basal position); nodal veinlet is normally oblique; subnodal veinlet very oblique and with a crossvein between it and RP1/2; pterostigma elongate, covering about twelve cells; microsculptures of pterostigma pyramid-like as in extant Epallaginae; pterostigma unbraced, basal side normally oblique, distal side strongly oblique; the pterostigma whitish and opaque, indicating a teneral specimen; two rows of cells in postnodal area distal to pterostigma for a distance of three cells; numerous postnodal crossveins, not aligned with corresponding postsubnodal crossveins; basal brace

Ax0 preserved; two primary antenodal crossveins, Ax1 and Ax2, aligned and stronger than other (secondary) antenodals; Ax1 0.6 mm basal to arculus, and Ax2 2.3 mm distal to Ax1; three secondary antenodal crossveins between Ax1 and Ax2 in first row, but none in second row; fifteen secondary antenodal crossveins visible between costal margin and ScP distal to Ax2; antenodal area between ScP and RA distal to Ax2 definitely free of crossveins, except a single weak crossvein below the fourth secondary antenodal of the first row; twenty-three antesubnodal crossveins (incl. one between subnodus and RP); two antesubnodal crossveins basal to midfork; no antefurcal crossveins between basal parts of RP and MA; RP and MA widely separated at their origins at arculus; arculus situated much basal to Ax2 (very close to Ax1); arculus rather straight and bridged by a strongly developed arcular bracket; discoidal cell 1.5 mm long, more or less rectangular, and free of crossveins; distal side (MAb) of discoidal cell and subdiscoidal veinlet (CuA) of reversed obliquity, strictly aligned, and bridged by a strongly developed discoidal bracket (= medio-anal link *sensu* Fraser, 1955; = discal brace *sensu* Carle, 1982); basal space free of crossveins; subbasal space only traversed by CuP-crossing (= anal-crossing *sensu* Fraser, 1957), 0.2 mm basal to arculus; subdiscoidal cell free of crossveins; vein RA slightly bulged and thickened along pterostigma; first furcation of RP (midfork) shifted to a very basal position, somewhat basal to Ax2; RP1/2 is curved towards RA at its origin; origin of RP2 not aligned with subnodus, but situated about one cell distal to it; RP1 slightly bulged beneath pterostigma; RP2 distinctly diverging from RP1 (both veins basally separated by a single row of cells up to the seventh cell, and separated by about nine rows of cells near wing margin); five strong intercalary veins between RP1 and RP2 that are alternating concave and convex; IR1 is the long and convex intercalary in the middle of the area between RP1 and RP2; no lestine oblique vein "O" between RP2 and IR2; IR2 originates 0.5 mm distal to midfork, only separated by a single cell from origin of RP3/4; distally IR2 is about in the middle of the broad area between RP2 and RP3/4, which also contains numerous intercalary veins that are alternating concave and convex (two strong intercalaries between RP2 and IR2, and four strong intercalaries between IR2 and RP3/4); MA smoothly curved and distally strongly diverging from RP3/4 with numerous intercalary veins between them; MP sigmoidally curved and distally right in the middle of the broad area between MA and CuA, which also contains numerous intercalary veins; postdiscoidal area basally very narrow with only one row of cells up to the level of nodus, but distinctly widened distally, although less so than in *Litheuphaea carpenteri*; postsubdiscoidal area between MP and CuA basally narrow with only one row of cells, but widened distally with three rows of cells; CuA sigmoidally curved, and ending on the level of nodus; cubito-anal area narrower than in *Litheuphaea carpenteri*, with max. five rows of cells and only one concave intercalary vein ("accessory anal vein"); anal area with max. three rows of cells; wing base hardly stalked; no membranule visible.

Left hind wing

Only a small basal fragment preserved that is similar to the left fore wing in all visible features, except for the presence of three secondary antenodals in the first row between Ax1 and Ax2, and the presence of only one antesubnodal crossvein basal to midfork. The area distal to discoidal cell and the largest part of the cubito-anal and anal areas are missing. Distance from base to arculus, 2.8 mm; from base to midfork, 4.0 mm; Ax1 0.3 mm basal to arculus, and Ax2 1.9 mm distal to Ax1.

Right fore wing

Similar to left fore wing in all preserved features (incl. origin of RP2 one cell distal to subnodus), except for the presence of four secondary antenodal crossveins in the first row between the two primaries Ax1 and Ax2; the absence of any secondary antenodals between ScP and RA distal to Ax2; the presence of three antesubnodal crossveins basal to midfork; and the subdiscoidal cell being divided by a single crossvein. Distance from base to nodus, 11.6 mm; from base to arculus, 3.1 mm; from base to midfork, 4.6 mm; Ax1 0.7 mm basal to arculus, and Ax2 2.2 mm distal to Ax1; length of discoidal cell, 1.6 mm; RP2 originates about one and a half cell distal to subnodus.

Right hind wing

The distal part of the fragment is exposed on the external surface of the amber piece. Venation similar to left fore wing in all preserved features, except for the presence of only two secondary antenodal crossveins in the first row between Ax1 and Ax2; the presence of four rows of cells in the anal area below the subdiscoidal cell; and a more distinctly developed accessory vein in the cubito-anal area (because of the distortion of this area, the corrugation of the accessory vein cannot be determined, but it seems to be rather neutral). Distance from base to arculus, 2.9 mm; from base to midfork, 4.0 mm; Ax1 0.6 mm basal to arculus, and Ax2 1.8 mm distal to Ax1; length of discoidal cell, 1.2 mm.

Systematic position

The presence of numerous antenodal crossveins, the non-alignment of the postnodal crossveins with the postsubnodal crossveins, the very elongate and unbraced pterostigma, and the rectangular discoidal cell, clearly indicate a position within Caloptera (*sensu* Bechly, 1996a; = Calopterygoidea auct.). The strongly developed dorsal discoidal bracket and the reversed obliquity of the distal side of the very short discoidal cell (aligned with the subdiscoidal veinlet), as well as the vestigial petiolus, the sigmoidal curvature of vein CuA, and the pyramid-type of microsculptures on the pterostigma, indicate a position in Epallagoidea. A position in Epallagidae is indicated by the basal curvature of vein RP1/2 towards RA, and the basal position of the arculus (basal to Ax2), while the hypertrophied anal area and the accessory "anal" vein indicate a position in the fossil subfamily Eodichromatinae. This systematic position is also supported by the absence of the autapomorphies of the extant subfamily Epallaginae (crown-group). The suppression of all secondary antenodals between ScP and RA is a distinct and unique synapomorphy of *L. ludwigi* and *L. carpenteri*, which allows an attribution to the same genus Litheuphaea, especially considering the overall similarity of the two species.

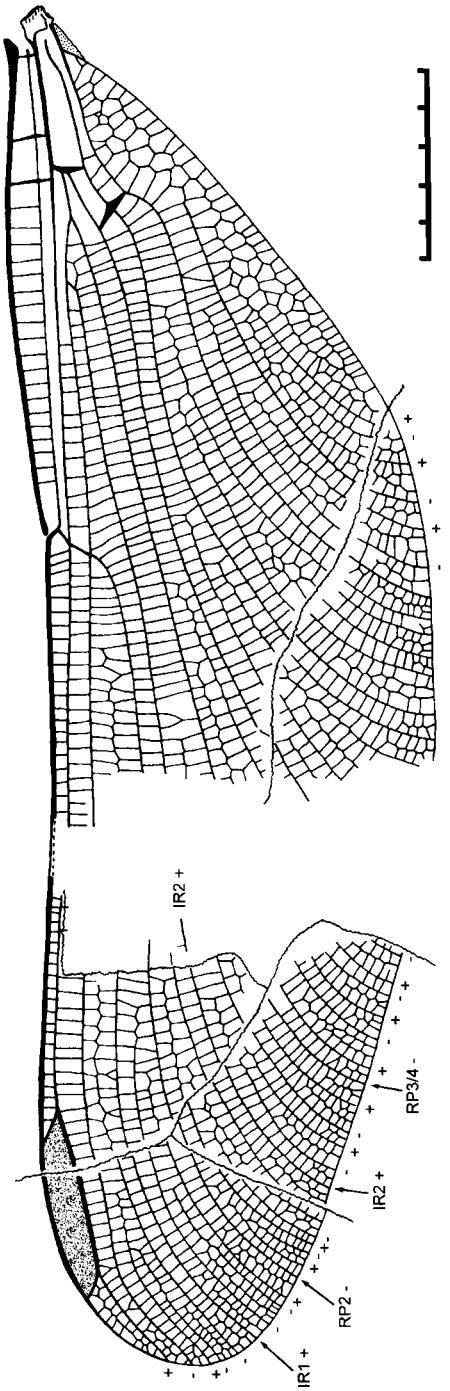


Fig. 9: *Litheuphaea carpenteri*, holotype specimen [No. 4895a] MCZ, Cambridge, U.S.A. (camera lucida drawing). [Scale 5 mm]

Litheuphaea carpenteri Fraser, 1955
Figure 9

*1955 *Litheuphaea carpenteri* Fraser, pp. 42-44, text-fig. 1.
1988 *Litheuphaea carpenteri*; Nel, pp. 175-179.
1992 *Litheuphaea carpenteri*; Carpenter, p. 88, text-fig. 52/5.
1992 *Litheuphaea carpenteri*; Nel & Paicheler, p. 385.
1994 *Litheuphaea carpenteri*; Bridges, pp. III.27 and VII.45.

Material. -Holotype: Specimen No. 4895a/b in collection Carpenter of the Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. (collected by C.W. Washburne).

Stratum typicum. -Tertiary, Middle Oligocene, Eugene Formation.

Locus typicus. -3 miles north of Goshen, Oregon, U.S.A.

New differential diagnosis. -This species is distinguished from *Litheuphaea ludwigi* sp. n. by the following characters: More dense wing venation, with more numerous cells and intercalary veins (autapomorphy ?); subdiscoidal cell divided by two crossveins; four cells between the origins of IR2 and RP3/4; base of RP1/2 not distinctly curved towards RA (reversal ?); RP2 aligned with subnodus; broader postdiscoidal, postsubdiscoidal, cubito-anal, and anal areas, with more rows of cells (see Figure 9); arculus angled and in a more distal position, closer to Ax2 than to Ax1; subnodal veinlet less oblique than nodal veinlet; basal side of pterostigma more strongly oblique, and with a crossvein between it and costal margin; fifteen cells beneath pterostigma; all cells between costal margin and RA distal to pterostigma are double, except for the two apical ones.

L. carpenteri differs from *Parazacallites aquisextanea* Nel, 1988 in its larger size (wing length 34 mm instead of only 21.5 mm); much more dense wing venation, with more numerous cells and more intercalary veins; more distal position of arculus (closer to Ax2 instead of aligned with Ax1); absence of any secondary antenodal crossveins between ScP and RA; presence of five cells between the origins of IR2 and RP3/4, instead of only one cell; subdiscoidal cell being divided by two crossveins; and its different pattern of intercalary veins in cubito-anal area.

L. carpenteri differs from *Eodichroma mirifica* Cockerell, 1923 in its larger size (wing length 34 mm instead of only 20 mm); much more dense wing venation, with more numerous cells and more intercalary veins; absence of typical bicolored wing pattern of *Eodichroma*; absence of unique triadic branching of accessory veins in cubito-anal area; and its more basal position of nodus (at 38 % instead of 42 %).

Redescription

The original drawing of Fraser (1955) obviously represents a reconstruction rather than a precise drawing of the holotype, and contains several important errors (especially in the antenodal and antefurcal area) that hamper the recognition of the true phylogenetic position of this fossil species. Contrary to the statement of Fraser (1955), it is by no means certain that this wing indeed represents a fore wing; it could as well be a hind wing.

The holotype represents the imprint and counter-imprint of a well-preserved damselfly

wing, of which only a middle part of the distal half of the wing is destroyed. The fossil was broken into several pieces that have been glued together again. The wing is preserved in a tuffaceous mudstone and deeply stained dull brown. The wing venation is generally dense with numerous cells and many intercalary veins.

Length, 34.0 mm; max. width, 9.5 mm (not 10.5 mm as stated by Fraser, 1955); distance from base to arculus, 3.5 mm; from base to midfork, 4.9 mm; from base to nodus, 12.8 mm; from nodus to the basal end of the pterostigma, 14.5 mm; length of pterostigma, 4.2 mm (not 5.15 mm as stated by Fraser, 1955); max. width of pterostigma, 1.0 mm; pterostigma very large and elongate, covering about fifteen cells; pterostigma unbraced, basal side very oblique with a crossvein between it and costal margin; nodus in a relatively basal position at 38 % of wing length; nodal veinlet distinctly more oblique than subnodal veinlet; two rows of cells in postnodal area distal to pterostigma; numerous postnodal crossveins (total number probably about fifty), not aligned with corresponding postsubnodal crossveins; basal brace Ax0 preserved; two primary antenodal crossveins, Ax1 and Ax2, aligned and stronger than other (secondary) antenodals; Ax1 0.8 mm basal to arculus, and Ax2 only 1.1 mm distal to Ax1; no secondary antenodal crossveins between Ax1 and Ax2; nineteen secondary antenodal crossveins visible between costal margin and ScP distal to Ax2 (thus the total number of visible antenodals is twenty-one, not twenty-seven as stated by Fraser, 1955, but there could have been two or three additional antenodals at the distal end of the antenodal space); no antenodal crossveins in the second row between ScP and RA distal to Ax2 (clearly visible on both parts, contrary to Fraser, 1955, who's erroneous drawing and statement that the subcostal and costal antenodals shall be strictly aligned, are probably based on an incorrect extrapolation from the two primary antenodals); basal half of antesubnodal area apparently free of crossveins, too, contrary to the drawing of Fraser (1955); no antefurcal crossveins between basal parts of RP and MA, contrary to the drawing of Fraser (1955); RP and MA distinctly separated at their origins at arculus; arculus situated somewhat basal to Ax2; arculus angled and bridged by a strongly developed arcular bracket; discoidal cell very short (mean length, 1.4 mm; mean width, 0.4 mm), more or less rectangular, and free of crossveins; distal side (MAb) of discoidal cell and subdiscoidal veinlet (CuA) of reversed obliquity, strictly aligned, and bridged by a strongly developed discoidal bracket (= medio-anal link *sensu* Fraser, 1955; = discal brace *sensu* Carle, 1982); basal space free of crossveins; subbasal space only traversed by CuP-crossing (= anal-crossing *sensu* Fraser, 1957), 0.2 mm basal to arculus; subdiscoidal cell divided by two crossveins (the alleged presence of at least four "cubital crossveins" was another erroneous interpretation by Fraser, 1955); vein RA slightly bulged and thickened along pterostigma; first furcation of RP (midfork) is shifted to a very basal position; RP1/2 not distinctly curved towards RA at its origin (contrary to extant Epallagidae); origin of RP2 aligned with subnodus; RP1 slightly bulged beneath pterostigma; RP2 distinctly diverging from RP1 (both veins basally separated by a single row of cells up to the eighth cell, and separated by about twenty cells at wing margin); five strong intercalary veins between RP1 and RP2 that are alternating concave and convex; IR1 is the long and convex intercalary in the middle of the area between RP1 and RP2; no lestine oblique vein "O" between RP2 and IR2; IR2 originates 1.6 mm distal to midfork; area between origins of IR2 and RP3/4 short and divided into five cells (contrary to the original drawing of Fraser, 1955); distal part of IR2 is about in the middle of the broad area between RP2 and RP3/4, which also contains numerous intercalary veins that are

alternating concave and convex (two strong intercalaries between RP2 and IR2, and four strong intercalaries between IR2 and RP3/4); MA smoothly curved and distally strongly diverging from RP3/4, with numerous intercalary veins between them; MP strongly sigmoidally curved and distally running right in the middle of the broad area between MA and CuA, which also contains numerous intercalary veins; postdiscoidal area basally very narrow with only one row of cells up to the level of nodus, but much widened distally; postsubdiscoidal area between MP and CuA basally narrow with only one row of cells, but distally widened with numerous rows of cells (MP and CuA separated by thirteen cells at wing margin); CuA strongly sigmoidally curved and reaching beyond the level of nodus; CuA separated from the accessory concave "anal" vein by seven cells at wing margin; cubito-anal area very broad with numerous (up to ten) rows of cells and several intercalary veins, including a strong accessory concave "anal" vein; anal area with three to four rows of cells (there is definitely no "recurrent anal vein" in this area, contrary to the statement of Fraser, 1955); wing base hardly stalked; there seems to be a tiny membranule, which is also present in extant calopterygoid damselflies according to Bechly (1996a).

Discussion

Phylogenetic systematics of fossil Euphaeida

Euphaeida Bechly, 1996

*1996 Euphaeida Bechly (taxon nov.) (corresponding to Euphaeoidea *sensu* Heymer, 1975)

Phylogenetic definition. – The most inclusive clade that contains *Epallage fatime* (Charpentier, 1840) and *Polythore gigantea* (Selys, 1853) but neither *Calopteryx virgo* (Linnaeus, 1758), nor any of the type-species of the other type-genera of the non-euphaeidan family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included taxa. – Epallagoidea and Polythoridae. The sister-group of Euphaeida is Calopterygida (*sensu* Bechly, 1996a), including the sister-groups Heliocharitidae and Calopterygoidea. The latter are comprising the sister-families Caliphaeidae and Calopterygidae (incl. Hetaerininae and Calopteryginae).

Autapomorphies. – More strongly developed dorsal discoidal bracket on distal side MAb of discoidal cell and subdiscoidal vein (basal CuA); larvae with 6-7 pairs of ventro-lateral abdominal gills (6 pairs on segments 2-7 in Polythoridae and 7 pairs on segments 2-8 in Epallagidae, but the polarity of this difference is unclear; the abdominal gills are secondarily absent in some genera of Epallagidae, e.g. *Anisopleura*).

Polythoridae Munz, 1919

1853 légion Thore Selys (clearly not a valid family-group taxon according to Art. 11f IRZN)

1954 Irregulières Selys (taxon nov., but no family-group taxon)

1903 Thorinae Needham (objectively invalid name since based on a homonym type-genus)

*1919 Polythorinae Munz (subfam. nov.)

1939 Polythoridae; Tillyard & Fraser (stat. nov.)

Type-genus. – Polythore Calvert, 1917 nom. subst. pro Thore Selys, 1853, nec Thore Kock, 1850.

Phylogenetic definition. – The least inclusive clade that contains all extant species that are closer related to *Polythore gigantea* (Selys, 1853) than to *Epallage fatime* (Charpentier, 1840) (node-based definition of crown-group).

Included taxa. – Euthorinae and Polythorinae (incl. Miocorini and Polythorini *sensu* Bechly, 1996a).

Autapomorphies. – Distal half of wings distinctly broadened; discoidal cell touches RA (convergent to Lestinae), because the arculus is only formed by the basal discoidal crossvein (= posterior arculus) that is developed as an apparent branch of [M & Cu] (unique type of arculus within Odonatoptera); insertion of arcular crossvein on [RP & MA] of secondary type (convergent to Eulestiformia *sensu* Bechly, 1996a); dorsal arcular bracket reduced (convergent to Lestidae and Eurypalpida); basal space traversed by numerous crossveins (convergent to most Calopterygidae); subbasal space (cubital cell and subdiscoidal cell) traversed by numerous crossveins (convergent to most Calopterygoidea), so that the CuP-crossing (= anal crossing *sensu* Fraser, 1995) is unidentifiable; discoidal cell traversed by several crossveins (convergent to Calopterygidae); 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 (convergent to Calopterygidae), with a concave intercalary vein between these branches (triadic branching; reversed in Miocorini); adult males with four lobes of unique shape (the lateral ones having a filamentous apex) on the terminal segment of the ligula (Kennedy, 1919); adult males with reduced paraprocts; resting position with wings closely apposed over the dorsum of the body (also occurring within Epallaginae); larvae with several angular projections on the saccoid caudal gills.

Epallagoidea Needham, 1903 (stat. nov.)

1975 Euphaeoidea; Heymer (stat. et sens. nov.)

1996 Euphaeoidea; Bechly (sens. nov.)

Type-genus. – Epallage Charpentier, 1840.

Phylogenetic definition. – The most inclusive clade that contains *Epallage fatime* (Charpentier, 1840) but neither *Polythore gigantea* (Selys, 1853), nor any of the type-species of the other type-genera of the non-euphaeidan family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included taxa. – Zacallitidae and Epallagidae.

Autapomorphies. – Wing venation more densely reticulated (convergent to Polythorinae and Calopterygidae); petiolus shortened (Fraser, 1940; convergent to Calopterygidae); discoidal cell very short (Fraser, 1940); distal discoidal vein MAb and subdiscoidal vein with reversed obliquity (convergent to Calopterygidae); CuA sigmoidally and smoothly curved (Fraser, 1940); curved intercalary veins between CuA and hind margin (Fraser, 1940); [M & Cu] or MP not kinked or bent at arculus (convergent to Calopterygoidea); thorax and abdomen relatively strong and stout, rather anisopterid-like (not yet known from Eodichromatinae).

Zacallitidae Cockerell, 1928 (stat. rest.)

*1928 Zacallitidae Cockerell (fam. nov.)

1940 Zacallitidae; Fraser (pos. nov.)

1992 Zacallitidae; Carpenter (treated as junior subjective synonym of Epallagidae)

1994 Zacallitidae; Bridges (treated as junior subjective synonym of Epallagidae)

1996 Zacallitidae; Bechly (sens. nov.)

Type-genus. – *Zacallites* Cockerell, 1928.

Phylogenetic definition. – The most inclusive clade that contains *Zacallites balli* Cockerell, 1928 but neither *Epallage fatime* (Charpentier, 1840), nor any of the type-species of the other type-genera of the family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included taxa. – Only including the single fossil species *Zacallites balli* Cockerell, 1928 from the Upper Eocene (Green River) of Colorado, U.S.A. (the holotype probably was in the collection of Dr Oscar Melville Ball in the disbanded Museum of the Biology Department of the Agricultural and Mechanical College of Texas; the present location is unknown). A redescription of the holotype, together with a precise drawing of the wing venation, would be most important, since the only published drawing by Fraser (1940) is an unreliable reconstruction rather than a precise drawing of the fossil.

Autapomorphies. – Apex of both wings dark coloured; base of IR2 widely separated from midfork (convergent to Philoganginae and Epallaginae); cubito-anal area secondarily expanded (convergent to Eodichromatinae, or a symplesiomorphy ?); hind wing with accessory convex intercalary "anal" vein (certainly not homologous with the concave intercalary "anal" vein in Eodichromatinae).

Epallagidae Needham, 1903

1853 légion Euphaea Selys (not a valid family-group taxon according to Art. 11f IRZN)

1954 Planinases [partim] Selys (taxon nov., but no family-group taxon)

*1903 Epallaginae Needham (subfam. nov.)

1905 Euphaeinae Jacobson & Bianchi (subfam. nov. with the type-genus Euphaea Selys, 1840; = Euphaea Rambur, 1842, junior objective synonym and homonym; = Pseudophaea Kirby, 1890, erroneous nom. subst. pro Euphaea Rambur, 1842, nec Euphaea Selys, 1840, junior objective synonym) (new junior subjective synonym)

1906 Epallagidae; Handlirsch (stat. nov.) (nom. transl. ex Epallaginae Needham, 1903)

1917 Epallaginae Tillyard (subfam. nov.) (junior objective synonym and homonym)

1917 Epallagini Tillyard (trib. nov.) (junior objective synonym and homonym)

1939 Epallagidae; Tillyard & Fraser (stat. et sens. nov.) (nom. transl. ex Epallaginae Tillyard, 1917) (junior objective synonym and homonym)

1959 Euphaeidae; Montgomery (stat. nov.)

1981 Epallaginidae; Davies (incorrect subsequent spelling)

1992 Euphaeidae; Carpenter (sens. nov.)

1996 Euphaeidae; Bechly (sens. nov.)

Type-genus. – *Epallage* Charpentier, 1840.

Phylogenetic definition. – The most inclusive clade that contains *Epallage fatime* (Charpentier, 1840) but neither *Zacallites balli* Cockerell, 1928, nor any of the type-species of the other type-genera of the non-euphaeidan family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included taxa. – Eodichromatinae and Epallaginae.

Autapomorphies. – Antenodal crossveins more numerous, and both rows of antenodal

crossveins strictly aligned (convergent to Calopterygoidea and Eurypalpida); at least a smooth basal curving of RP1/2 towards RA (convergent to many Chlorocyphoidea and all Calopterygida); arculus shifted basally between Ax2 and Ax1 (convergent to Calopterygida; evidenced by the referring character states in Eodichromatinae and Heliocharitidae, while the states cannot be determined in Epallaginae and Calopterygoidea); microsculpture of pterostigmata consisting of tiny pyramid-like structures (convergent to *Devadatta*, Chlorocyphoidea and Platystictidae; not yet known in Zacallitidae).

Eodichromatinae Cockerell, 1923 (nom. correct. et sens. nov.)

*1923 Eodichrominae Cockerell (subfam. nov.)

1928 Parazacallitinae Nel (subfam. nov.) (here regarded as new junior subjective synonym)

1994 Parazacallitinae; Bridges (treated as junior subjective synonym of Chlorocyphidae)

Type-genus. – *Eodichroma* Cockerell, 1923.

Phylogenetic definition. – The most inclusive clade that contains *Eodichroma* Cockerell, 1923 but neither *Epallage fatime* (Charpentier, 1840), nor any of the type-species of the other type-genera of the non-euphaeidan family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included Taxa. – Eodichromatini and Litheuphaeini.

Autapomorphies. – Cubito-anal area secondarily expanded (convergent to Zacallitidae ?), with an unique accessory concave "anal" vein (intercalary) between CuA and the hind margin; Ax1 and Ax2 closely approximated; no antefurcal crossveins between basal parts of RP and MA.

EodichromatinI Cockerell, 1923 (stat. nov.)

Type-genus. – *Eodichroma* Cockerell, 1923.

Phylogenetic definition. – The most inclusive clade that contains *Eodichroma* Cockerell, 1923 but neither *Litheuphaea carpenteri* Fraser, 1955, nor any of the type-species of the other type-genera of the non-euphaeidan family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included genera. – *Eodichroma* and *Parazacallites.*

Autapomorphies. – Anal area with a unique recurrent intercalary vein parallel to anal vein beneath subdiscoidal cell; small size (wing length only 20-21.5 mm).

Eodichroma Cockerell, 1923

Included species. – Only including the fossil type-species *Eodichroma mirifica* Cockerell, 1923 from the Upper Eocene kaolinite of Jackson, Texas, U.S.A. (holotype was in the collection Dr Oscar Melville Ball in the Museum of the Biology Department of the Agricultural and Mechanical College of Texas). A redescription of the holotype, together with a precise drawing of the wing venation, would be most important, since the only published illustration is a photograph within the brief original description. Unfortunately the present location of the holotype is unknown, since the referring Museum was disbanded and the collections given to other universities (pers. comm. by Mrs. Lynne Hambric, Education Reference Librarian of the Sterling C. Evans Library, TAMU).

Autapomorphies. – Characteristical pattern of intercalary veins in the cubito-anal area that form a asymmetrical triadic fork with CuA (quite different from the symmetrical triadic fork in Polythoridae, thus probably no putative synapomorphy); basal half of wing dark coloured.

Parazacallites Nel, 1988

Included species. – Only including the fossil type-species *Parazacallites aquisextanea* Nel, 1988 from the Upper Oligocene of Aix-en-Provence in France (holotype specimen No. IPM-R06688 in collection Saporta at the Paleontological Institute of the Muséum National d'Histoire Naturelle in Paris).

Autapomorphies. – Arculus shifted basal to Ax1; pattern of secondary veins in the cubito-anal area.

Litheuphaeini Bechly, 1996 (pos. nov.)

*1996 Litheuphaeini Bechly (trib. nov.)

Type-genus. – *Litheuphaea* Fraser, 1955.

Phylogenetic definition. – The most inclusive clade that contains *Litheuphaea carpenteri* Fraser, 1955 but neither *Eodichroma* Cockerell, 1923, nor any of the type-species of the other type-genera of the non-euphaeidan family-group taxa *sensu* Bechly (1996a) (stem-based definition).

Included genera. – Only including the type-genus *Litheuphaea.*

Autapomorphies. – Same as for type-genus (see below).

Litheuphaea Fraser, 1955

Included species. – Only including the fossil type-species *Litheuphaea carpenteri* Fraser, 1955 and its new fossil sister-species *Litheuphaea ludwigi* sp. n.

Autapomorphies. – All secondary antenodals between ScP and RA suppressed (convergent to Amphipterygida *sensu* Bechly, 1996a).

Epallaginae Needham, 1903 (sens. nov.)

1996 Euphaeini; Bechly (sens. nov.)

Type-genus. – *Epallage* Charpentier, 1840.

Phylogenetic definition. – The least inclusive clade that contains all extant species that are closer related to *Epallage fatime* (Charpentier, 1840) than to *Polythore gigantea* (Selys, 1853) (node-based definition of crown-group).

Included taxa. – Including all extant genera of Epallagidae (enumerated in Bridges, 1994).

Autapomorphies. – Base of IR2 widely separated from the midfork (convergent to Philoganginae and Zacallitidae); base of RP1/2 strongly curved towards RA, arising on RP with a secondary insertion (convergent to many Chlorocyphoidea and all Calopterygida); all antenodals developed as enforced brackets, so that the two primary antenodals can no longer be distinguished from the secondary antenodals (convergent to Calopterygoidea and many Eurypalpida); numerous macrotrichae on the dorsal surface of the wing vein ScP (unknown in the fossil Euphaeida and therefore maybe an autapomorphy for a more inclusive monophylum); lateral lobes of larval prehensile mask with only two endhooks (unknown in the fossil Euphaeida and therefore maybe an autapomorphy for a more

inclusive monophylum).

Other alleged fossil Euphaeida

Euphaeopsis Handlirsch, 1906 and the four species of *Pseudoeuphaea* Handlirsch, 1906 from the Upper Jurassic Solnhofen Limestone have to be regarded as nomina dubia, since the referring holotypes are all lost, and the original descriptions and existing figures of these type specimens are rather useless. These taxa may not represent Epallagidae at all, but could rather belong to the Mesozoic family Steleopteridae (Nel & Bechly & Martínez-Delclòs, in prep.) which is either a basal group of Zygoptera - Caloptera, or a member of the "anisozygopterous" grade (maybe Epiophlebioptera according to Bechly, 1997).

Epallagites avus Cockerell, 1924 from the Eocene of Colorado (Green River) is only known by a poorly preserved small fragment and thus should be preliminarily regarded as a Zygoptera - Caloptera incertae sedis (Carpenter, 1992; Nel & Paicheler, 1992) until better preserved material becomes available.

Genuine fossil Epallagidae - Epallaginae may be a wing fragment from the Upper Miocene of Italy, described as *Epallage* spec. by Cavallo & Galleti (1987), and a fossil damselfly from the Oligocene of France, described as *Indophaea* spec. by Théobald (1937) (also see Nel & Paicheler, 1992; and Carpenter, 1992).

Paleobiogeography

Extant Epallagidae are only known from the subtropical (incl. Mediterranean and Middle East regions) and tropical regions of Eurasia, especially the Indo-Malayan region, while fossil stem-group representatives are known from North America and Middle Europe. The extant sister-group is Polythoridae according to Bechly (1996a, 1997) and is endemic to the Neotropical region. This distributional pattern suggests that the present absence of extant Epallagidae from North America and Middle and Northern Europe is secondary, probably due to the significant climatic changes after the Eocene-Oligocene. Although the Epallagidae probably originated in the Lower Tertiary of the Northern Hemisphere, possibly in the Nearctic region, it obviously became extinct in North America before this group could invade the Neotropical region. The absence from Africa and Australia can thus far only be explained by mere contingency. The hypothesis of Fraser (1957: 78) that the Epallagidae could be of Oceanian origin is almost certainly erroneous, since it is based on the incorrect assumption that the Australian genus *Diphlebia* represents the closest relative of Epallagidae (compare Bechly, 1996a, 1997).

Taxonomy of the family-group name Epallagidae (versus Euphaeidae)

Like several other family-group taxa within Odonata, the authorship of Euphaeidae has often been attributed to Selys, 1853 who created the "légion *Euphaea*". Many subsequent authors endorsed Selys's authorship of the referring family-group taxa or even explicitly emphasised that the "légions" of Selys-Longchamps correspond to modern family-group taxa (e.g. Montgomery, 1962; Dunkle, 1991; Carpenter, 1992; Bridges, 1994). However, according to Art. 11(f)(i) IRZN it is evident that Selys's "légions" are not available as

family-group taxa, since they are neither "nouns in the nominative plural" (1), nor "ending in a latinized suffix" (3). Thus in the case of Euphaeidae Jacobson & Bianchi, 1905 are the correct authors, while Needham, 1903 is the author of Epallagidae. Consequently, Euphaeidae must be regarded as a junior subjective synonym of Epallagidae. Similarly the family-group name Dicteriadidae Montgomery, 1959 (nec Selys, 1853) must be replaced by the next available and valid senior subjective synonym Heliocharitidae Tillyard & Fraser, 1939 (*contra* Dunkle, 1991). The same will of course also apply to all the other attributions of authorship based on Selys "légions"!

Annotated catalogue of Odonata specimens in amber

Odonates in Dominican amber

The amber from the Dominican Republic originated in the Middle Eocene to Upper Oligocene (45-25 Mio. years b.p.), maybe even until the Lower and Middle Miocene (15-20 Mio. years b.p.). The Dominican "amber-tree" most probably has been a member of the extant genus *Hymenaea* (*H. protera* Poinar), a neotropical leguminous that is known for its high production of resin (Schlee, 1986). Amber from the Dominican Republic is extraordinary for the following three reasons:

a) Numerous places of discovery, with a large output of high-quality amber.

b) Regular findings of large pieces of amber, up to 13 kg!

c) Frequent and diverse inclusions: Plants (blossoms, leaves and bark), arachnids (incl. scorpions, amblypygids, and pseudoscorpions), insects (incl. odonates, mantids, membracids, strepsipteres, and fleas) and even vertebrates (mammal bones and bird feathers, as well as complete small frogs, geckos, and anolis-iguanas)! There are also single pieces of amber with "mass-catches" of insects, e.g. containing 2000 ants, or 1000 dolichopodid flies, or 15 moths etc.

Therefore it is certainly not over-optimistic to expect further odonates from Dominican amber in the future [please note: "Dominican amber" is a well-established term for Tertiary amber from the Dominican Republic, although it could theoretically be confused with (actually not existing) amber from the Caribbean island of Dominica].

The following seven fossil damselflies from Dominican amber are located in the "Museum am Löwentor des Staatlichen Museums für Naturkunde" in Stuttgart, Germany (Schlee, 1990 and pers. comm. 1993):

(1) A complete damselfly that is not well visible, because the insect is surrounded by dirt.

(2-4) A relatively large piece of amber, containing three (!) damselflies.

(5) A fragmentary damselfly-wing.

(6) A fine preserved distal half of a damselfly-wing in clear amber.

(7) A damselfly (head, thorax, legs, proximal abdomen and wing bases) in excellent condition, preserved in clear, polished amber.

These specimens are all still undescribed, but beautiful colour-photos of the last two mentioned specimens, probably Coenagrionidae, have been published in Schlee (1990: 83). Unfortunately the magnificent amber collection of the Stuttgart museum is currently (June 1998) not accessible for scientific studies, because of the unexpected retirement of Dr Schlee. This unfortunate situation will hopefully change in 1999.

There are only eleven other odonate specimens known from Dominican amber:

(8) Orr (1993) reported about a libelluloid-like dragonfly completely preserved in Miocene amber, certainly from the Dominican Republic. Its present deposition unfortunately is unknown and it has apparently never been illustrated or described (Orr, pers. comm. Nov. 1996). It would be important to find out its present location (if any readers should know something of its whereabouts, I would be most grateful for information), and verify whether this unique specimen indeed represents a genuine Tertiary amber fossil, or maybe just a more recent copal inclusion (copal = subfossil amber) or even a forgery.

(9) Donnelly (1993; and pers. comm. Nov. 1996) has a damselfly wing (similar to Telebasis) in amber from the Dominican Republic, too. It is in his private collection, but has never been illustrated or described.

(10) Poinar (1996) described a new species of the recent coenagrionid genus *Diceratobasis*) from a piece of Dominican amber that is located in the private collection of Jim Work (Ashland, Oregon, USA). The larvae of this species probably lived in phytotelmata of tank bromeliads.

*1996 *Diceratobasis worki* sp. n. Poinar, pp. 382-383.

(11-17) According to Grimaldi (pers. comm. 1998) a private collector in Italy who wants to stay anonymous, has seven specimens (fragmentary ones and complete ones) of damselflies in Dominican amber. According to Poinar (pers. comm. 1997) this collector also provided the beautiful specimen on loan for the exhibition "Amber - Window to the Past" in 1996 at the American Museum of Natural History in New York. This latter specimen was illustrated in Grimaldi (1996: 78) and represents a well-preserved and nearly complete damselfly (only the wing apices are missing).

(18) According to Walter Ludwig (pers. comm. 1998) a relatively large and complete odonate, perfectly preserved in a clear piece of Dominican amber, was located in the private collection Kölner who purchased the specimen from the trader Georg Dommel (Ambar del Caribe, Düsseldorf). Unfortunately the collector deceased and the current whereabouts of his collection are unknown.

Odonates in Baltic amber (incl. Saxonian amber)

The Baltic amber of eastern Europe originated in the Upper Eocene (ca. 40-50 Mio. years b.p.) of Scandinavia, but is found in secondary deposits of glauconitic sands ("blue earth") of the Upper Eocene to Lower Oligocene (ca. 30-40 Mio. year b.p.) at the Baltic coast. Based on the monograph of Conwentz (1890) the Baltic "amber-tree" has long been assumed to be an extinct conifer that has been named *Pinus* (or *Pinites*) *succinifera* Goepp., although this taxon is still undefined and could include five different species (Schlee, 1986). However, Katinas (1971) demonstrated that the Baltic amber was most likely produced by a cedar, close to the extant species *Cedrus atlanticus,* and maybe also by an araucaria of the genus *Agathis* (= kauri-pine).

Hagen (1854) mentioned five odonates and Handlirsch (1906-1980) mentioned six odonates from Baltic amber. Handlirsch's list was incomplete and contained several errors, which unfortunately have been frequently perpetuated, even recently by myself (Bechly, 1993), although they had already been corrected by Ander (1942). Unfortunately, the Odonata chapter in the well-known catalogue of amber fossils by Keilbach (1982: 208-209) is likewise incomplete and incorrect, and it contains additional errors, too. The following new list will hopefully correct these errors and provide many

new information:

(19-20) Two fossil damselflies of the famous "Königsberg amber collection" are now located in the "Geologisch-Paläontologisches Institut der Universität Göttingen", Germany (species A: No. 3 B 696; and species B: No. K 8088). These specimens were described and figured by Pfau (1975). They are well-preserved and seem to represent female specimens of two different unnamed species of Coenagrionoidea from the Upper Eocene. Pfau's suggestion that these fossils might belong to the extant family Platycnemididae is not supported by available evidence, so that these fossils should continue to be regarded as Coenagrionoidea *incertae sedis*. According to Pfau one of the species might be conspecific with *Platycnemis ? antiqua* (Pictet & Hagen, 1856).

1975 "Zygoptera - möglicherweise Platycnemididae"; Pfau, p. 1.

1982 "Platycnemididae spec. A. u. spec. B."; Keilbach, p. 209.

1990 "Platycnemididae, genre incertae sedis (Pfau, 1975)"; Nel & Papazian, p. 254.

1993 "... seem to represent two different platycnemidid species which are still unnamed."; Bechly, p. 14.

1996 "Plectrocnemididae [sic] (?)"; Wichard & Weitschat, p. 27.

(21-25) Four pieces of amber (with remains of five specimens of damselflies), of which three have been located in the collection Berendt of the "Paläontologisches Museum des Museums für Naturkunde der Humboldt-Universität" in Berlin, Germany. Pfau (1975) could only locate the two of these pieces in the Berlin museum. The location of the fourth specimen is unknown. One of the two remaining specimens is one piece (No. 16) with a basal wing fragment and a male and a female abdomen (figure 11). It probably represents the remains of a trapped pair, and the appendages of the male abdomen indicate that they belong to the same species as the second specimen (Pfau, 1975). The second piece contains a wing fragment without base and apex, head, all 6 legs but without coxae and tarsi, and the apex of a male abdomen (figure 10). The labels for both pieces are marked with a red spot, indicating original and/or type status. These two pieces undoubtedly represent originals of Pictet & Hagen (1856), so that they must be regarded as syntypes of "*Agrion antiquum*". The female specimen described by Pictet (1856: 79) is apparently lost, as already supposed by Pfau (1975). Pictet (1856: 79) already mentioned that the specific identity of piece No. 16 can not be deduced. Therefore I designate the second specimen (original of Hagen, 1856: 79) as lectotype of *Platycnemis ? antiqua* (figure 10). Specimen No. 16 is a paralectotype, even though its specific affinities with the lectotype cannot be demonstrated. This lectotype designation was already mentioned by Bechly (1996b), but since that referring work was published in an electronic online journal on the Internet, the designation is here repeated in case that the previous designation is regarded as taxonomically invalid according Art. 8 IRZN.

1848 *Agrion antiquum* Pictet; Hagen, p. 7 (nomen nudum; knows 2 specimens).

1850 *Agrion ? antiquum* Pictet; Hagen in Selys, pp. 357-358.

1850 *Platycnemis ? antiquum*; Selys, p. 366.

1854 "*Agrion antiquum* P. 3."; Hagen, p. 227.

1856 *Agrion antiquum*; Giebel, p. 273.

*1856 *Agrion antiquum* Pictet in Berendt, pp. 78-79, pl. vi, figs 4a-d & 5 (first valid description; knows 3 specimens).

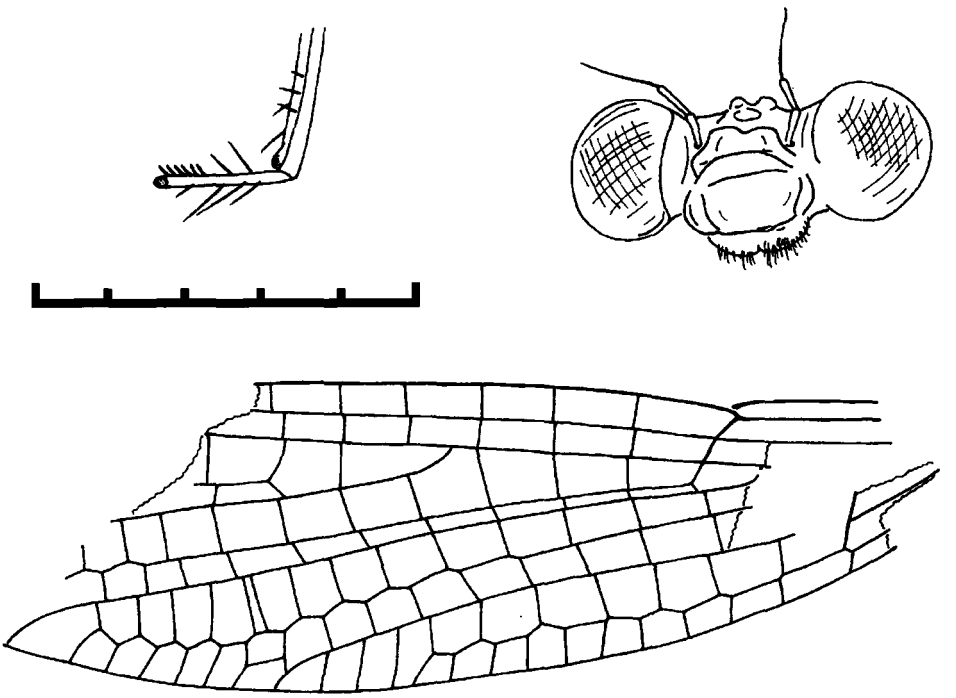


Fig. 10: *Platycnemis ? antiqua* (Pictet & Hagen, 1856), lectotype, in coll. Berendt, Museum für Naturkunde, Berlin, wing fragment, head, and right foreleg. The tibia of the fore leg is perspectively shortened in this figure (camera lucida drawing). [Scale 5 mm].

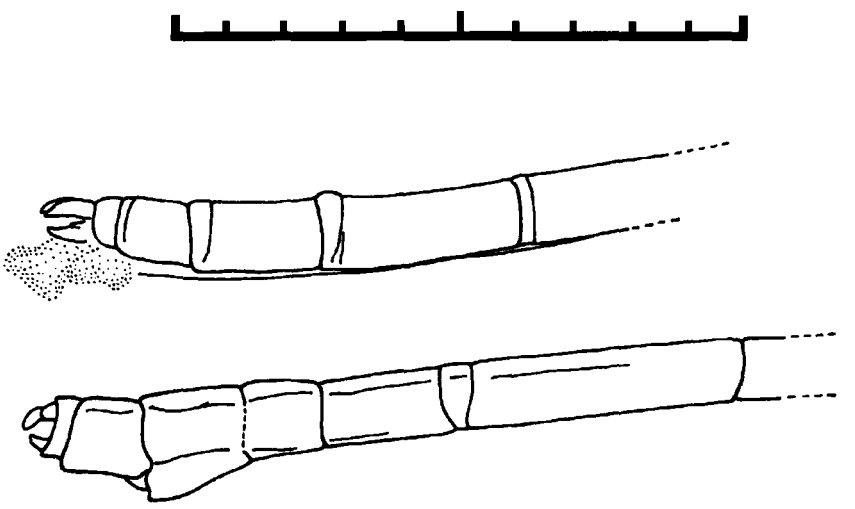


Fig. 11: *Platycnemis ? antiqua* (Pictet & Hagen, 1856), paralectotype specimen No. 16, in coll. Berendt, Museum für Naturkunde, Berlin. The "cloudy" structure at the end of the male abdomen is only an artifact, probably air bubbles(camera lucida drawing). [Scale 10 mm]

*1856 *Agrion antiquum* Hagen in Berendt, pp. 79-80, pl. viii, figs 11a-c (supplementary description; knows 4 specimens).

1890 *Coenagrion antiquum* Hag.; Kirby, p. 175.

1890 *Platycnemis antiquum*; Scudder, p. 127.

1908 *Platycnemis antiqua* Hagen; Handlirsch, p. 899.

1942 *Agrion antiquum* Pictet et Hagen 1856; Ander, p. 76 (states that the systematic position of this species is not yet certain).

1958 *Platycnemis ? antiqua* ?; Weidner, pp. 52-53.

1975 *Agrion antiquum* Pictet (= *Platycnemis antiqua* Hagen); Pfau, p. 4.

1978 *Platycnemis antiqua*; Larsson, p. 83.

1982 *Platycnemis antiqua* (Pictet & Hagen, 1856); Keilbach, p. 209.

1990 *Platycnemis antiqua* (Pictet & Hagen, 1856); Nel& Papazian, p. 254.

1993 *Platycnemis antiquum* (Pictet & Hagen), 1856; Bridges, p. VII.15.

1993 "Three *Platycnemis*-like damselflies, described by Hagen (1848, 1856) as *Platycnemis antiqua*"; Bechly, p. 14.

1994 *Platycnemis antiquum* (Pictet & Hagen), 1856; Bridges, p. VII.16.

1996 *Platycnemis antiqua* (Pictet & Hagen 1856); Wichard & Weitschat, p. 26.

(26) A piece of amber with one basal and two apical fragments of the wings of a relatively large dragonfly (wing span ca. 3 inches according to Hagen) in collection Menge. The present location is unknown. It has been named *Gomphoides occulta* by Hagen in Berendt (1856), but this name must be regarded as a nomen nudum, because Hagen did not provide a valid description (Art. 12 IRZN).

1854 *"Aeschna.* Flügelspitzen. – ... wahrscheinlich zu Gomphoides"; Hagen, p. 227.

1856 *Gomphoides occulta* Hagen; Hagen in Berendt, p. 81 (nomen nudum).

1890 *Gomphoides occulta* Hag.; Kirby, p. 168.

1908 *Gomphoides occulta* Hagen; Handlirsch, p. 900.

1921 *Gomphoides Selys;* Handlirsch, p. 217.

1942 "Aeschnidae s.l."; Ander, p. 77.

1957 "... *Gomphoides* ... have also been reported from Bavarian amber and the Miocene."; Fraser, p. 94.

1978 *Gomphoides occulta;* Larsson, p. 83.

1982 *Gomphoides occultus* Hagen, 1856; Keilbach, p. 209.

1992 *"Gomphoides* Selys-Longchamps in Selys-Longchamps & Hagen, 1850, p. 360 [Generic assignment of fossil doubtful.] Pictet & Hagen, 1856."; Carpenter, p. 81.

1993 *Gomphoides occulta* Hagen, 1856; Bridges, p. VII.167 (not treated as nomen nudum).

1993 "An adult dragonfly, described by Hagen (1854, 1856) as *Gomphus resinatus.*"; Bechly, p. 14.

1994 *Gomphoides occultus* Hagen, 1856 (in Berendt: 81); Nel & Paicheler, p. 60.

1994 *Gomphoides occulta* Hagen, 1856; Bridges, p. VII.170 (not treated as nomen nudum).

(27) A damselfly exuvia (Zygoptera) in collection Berendt. My recent (Nov. 1996) examination of this fossil in collection Berendt at the Paleontological Museum of the "Museum für Naturkunde" in Berlin (Germany), confirmed the redescription and conclusion of Hagen (1856). It is most probably an exuvia of a Coenagrionoidea *incertae sedis*. Conspecificity with *Platycnemis ? antiqua* (Pictet & Hagen, 1856) can not

be confirmed or denied by evidence. The figure of Pictet in Berendt (1856: pl. vi, fig. 6) is rather imprecise, e.g. showing the tarsi although they are not preserved, and not showing the ecdysial sutures although they are clearly preserved in the fossil. It believe it is unlikely that this exuvia was embedded at the original site of emergence, because: (a) It is a reasonable assumption that the conifer trees that produced the resin for the Baltic amber most probably were adapted for dry soils just like extant conifers, too, while damselfly larvae almost exclusively emerge on small plants that are directly adjacent to their breeding waters; and (b) the exuvia lacks all tarsi as well as the end of the abdomen with the caudal gills. The specimen is most likely an old exuvia that was blown (e.g. during a storm) into a blotch of resin and became embedded. However, two specimens of aquatic Gammaridae (Crustacea) are known from Baltic amber (Bachofen-Echt, 1949 (reprinted 1996): 42-44), of which at least one was embedded when it was still alive. Some aquatic habitats thus may have been close enough to the amber trees that such purely aquatic animals could become embedded, but on the other hand they might as well just be dropped by some predators (e.g. birds), which may be the most plausible explanation for the embedding of non-flying, purely aquatic organisms in amber. This might also explain the aquatic insect larvae (not exuviae!) described and figured in Wichard & Weitschat (1996).

1848 *Gomphus resinatus*; Hagen, p. 8 (nomen nudum; no description).

1850 "*Gomphus resinatus* Hagen, Nymphe"; Hagen in Selys, p. 358.

1852 *Gomphus resinatus* Hagen; Giebel, p. 639.

1854 "*Calopteryx* ?, Nymphenhaut."; Hagen, p. 227.

1856 *Libellula resinata*; Giebel, p. 284.

1856 "*Gomphus* - (larva)"; Pictet in Berendt, pp. 78 and 80, pl. vi, fig. 6 (first description).

1856 "*Agrionide*"; Hagen in Berendt, p. 80, pl. viii, fig. 12 (supplementary description and detailed figure of the mask; the term "Larva" in the explanation of fig. 12 refers to "*Agrion antiquum*").

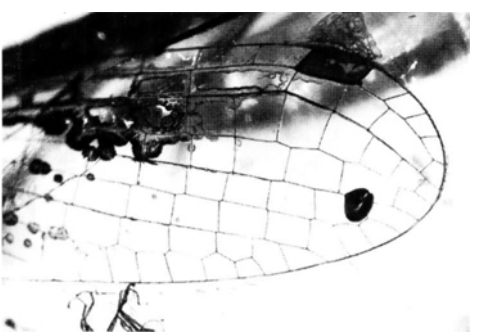


Fig. 12: *Platycnemis* ? *antiqua* (Pictet & Hagen, 1856), first specimen from Saxonian amber, specimen [without number] in coll. W. Ludwig, Berlin.

1890 *Aeschna resinata* Hag.; Kirby, p. 168.

1908 *Calopteryx* ? (larva) Hagen; Handlirsch, p. 896.

1908 *Gomphus resinatus* Hagen; Handlirsch, p. 900.

1908 *Gomphus* - (larva) Hagen; Handlirsch, p. 900.

1921 "Calopterygidae, zweifelhafte Larve"; Handlirsch, p. 217.

1921 "2 als Gomphus bezeichnete Formen"; Handlirsch, p. 217.

1942 "Agrioniden-Larve 1"; Ander, p. 76.

1957 "... *Gomphus* ... have also been reported from Bavarian amber and the Miocene."; Fraser, p. 94.

1982 "*Agrion spec.* Hagen in Berendt 1856, p. 80"; Keilbach, p. 209.

1982 "*Gomphus* Larva Hagen in Berendt 1856, p. 80"; Keilbach, p. 209.

1982 "*Gomphus resinatus* Pictet, 1856 in Berendt, p. 81"; Keilbach, p. 209.

1992 "*Gomphus* Leach, 1815, p. 37. [Generic assignment of fossil (nymph) doubtful.] Hagen, 1848."; Carpenter, p. 81.

1992 "*Calopteryx* Leach, 1815, p. 137. ... Hagen, 1848, ... Oligo., Europe (Baltic), ..."; Carpenter, p. 87.

1993 *Gomphus resinatus* Hagen, 1848; Bridges, p. VII.196 (not treated as nomen nudum).

1993 "A damselfly-larva (!) described by Hagen (1854) as *Calopteryx.";* Bechly, p. 14.

1993 "Another adult dragonfly, described by Hagen (1848, 1856) as *Gomphus resinatus.";* Bechly, p. 14.

1993 "A dragonfly larva (!), described by Hagen (1856) as *Gomphus.";* Bechly, p. 14.

1994 "*Gomphus resinatus* Pictet, 1856 (in Berendt, 1856: 81) (d'après Keilbach, 1982) ... Elle doit être considérée comme un Odonata Gomphidae (?) de position incertaine."; Nel & Paicheler, p. 57.

1994 "*Gomphus* "larva" Hagen, 1856 (in Berendt) ... Son attribution est très doubteuse."; Nel & Paicheler, p. 57.

1994 "*Gomphus resinatus* Hagen, 1848"; Bridges, p. VII.200 (not treated as nomen nudum).

(28) Another Zygoptera-larva in collection Hagen. I could not find this specimen in the amber collections of the Museum of Comparative Zoology in Cambridge (laboratory of late F.M. Carpenter), although most of the collection Hagen is presently located in this institution.

1850 "Agrion ... Une petite nymphe, ou plutôt l'étui vide."; Hagen in Selys, p. 357.

1856 "Eine unvollständige kleine Larve"; Giebel, p. 273.

1942 "Agrioniden-Larve 2"; Ander, p. 76.

(29) An odonate "larva" (certainly an exuvia) of uncertain affinities (location unknown; lost according to Ander, 1942):

1830 "*Libellula* -"; Berendt.

1856 "Libellenlarve"; Hagen in Berendt, p. 78.

1908 "Odonata incertae sedis. (Libellula) - Berendt."; Handlirsch, p. 904.

1942 "Odonaten-Larve incert. sedis"; Ander, p. 77 (this specimen might be identical with the specimen cited by Handlirsch (1906-1908) as Odonata incertae sedis).

1993 "A specimen classified by Handlirsch as Odonata incertae sedis, was described by Berendt (1830) as *Libellula* spec."; Bechly, p. 14.

(30) An undescribed abdomen of a female damselfly (completely preserved, incl. ovipositor) in collection Bachofen-Echt (Fach 2 L1A) at the "Bayerische Staatssammlung für Paläontologie und historische Geologie" in Munich, Germany. This specimen was illustrated by Bechly (1996b).

(31) A completely preserved damselfly in clear amber that is mentioned and figured by

Bachofen-Echt (1949 (reprinted 1996): p. 78 and fig. 63). The specimen is cited as Agrionidae (Wichard & Weitschat, 1996: 26; Poinar, 1992: 99), but almost certainly represents the only known member of Lestidae in amber, since the specimen has wings with an oblique vein and two cells beneath the distinctly braced pterostigma (clearly visible in the illustration of the original edition, but not well visible in the reprinted edition). I could not find the specimen in collection Bachofen-Echt in Munich (BSPGM), thus its present deposition unfortunately has to be regarded as unknown.

(32) Weidner (1958: 52) reports about a Zygoptera "larva" (*Platycnemis ? antiqua* ?) in a piece of Tertiary Baltic amber in collection Scheele (Nr. 1082. Typ. Kat. Nr. 45.) of the "Geologisches Staatsinstitut Hamburg", Germany. This specimen almost certainly represents an exuvia and not a true larva (Wichard & Weitschat, 1996).

(33-38) Walter Ludwig (Berlin, Germany) reported (pers. comm. 1996) a damselfly wing in a piece of Saxonian amber from Bitterfeld in the private collection of Hans Werner Hoffeins (Hamburg), and a complete damselfly in Baltic amber in the collection of the fossil trader Kühn was shown in Berlin. Furthermore Walter Ludwig has four specimens in his private collection in Berlin. One specimen is a fragment of a damselfly thorax with two wing bases and a nearly complete wing of a stem-group representative of Epallagidae (described here). Another unique specimen represents a damselfly just emerging from its exuvia (briefly described here), both completely preserved in a "Schlaube". These two specimens are from Baltic amber. The third specimen is a piece of amber with head (with deeply fissured labium) and one fore leg (with cleaning "brush") of an unidentified damselfly from the Saxonian amber of Bitterfeld (Eastern Germany). The fourth and most recently discovered specimen (figure 12) is from Saxonian amber, too, and represents two nearly complete wings and a few leg fragments that totally agree with the original description and the lectotype of *Platycnemis ? antiqua* (Pictet & Hagen, 1856). The tarsal claws of this specimen have a small claw hook. According to Weitschat (1996) the amber of Bitterfeld is of the same age and origin as the Baltic amber, not of Lower Miocene age (ca. 22 mybp) as previously believed. This would be supported by the occurrence of the same damselfly species *Platycnemis ? antiqua* in both "types" of amber.

(39) Hans Lüdicke (Kronberg, Germany) has a well-preserved and nearly complete damselfly (about 40 mm long) from the Baltic amber in his private collection. This specimen is currently being studied by Prof. Rainer Rudolph (Münster, Germany).

(40-41) Two damselflies from the Baltic amber are in the collection of the amber-museum at Ribnitz-Damgarten (East Germany). According to Ulf Erichson (pers. comm. 1997) one specimen is a wing and a body fragment in a piece of amber that was later manufactured as piece of jewellery. The second specimen is a nearly complete damselfly, but the amber contains some dirt, and furthermore the piece had to be glued after it was accidentally broken.

(42) A pair of damselfly wings in Baltic amber figured in Wichard & Weitschat (1996: 79, Taf. 3) and considered as a species of Lestidae (?) because of the elongate pterostigma and the strongly zigzagging vein MA. However, the pterostigmal brace is not visible, there is only one row of cells between the main wing veins, and there are no accessory intercalary veins (except IR1 and IR2), and the lestine oblique vein seems to be absent. All these characters contradict a position in Lestidae. Unusual features of this specimen are the extremely narrow space between RP1 and RP2, and the very long vein MA that even reaches beyond the distal end of the pterostigma, while MP reaches up to the

level of the distal end of the pterostigma, and the zigzagging CuA reaches up to the level of the basal end of the pterostigma. This combination of characters does not occur in any extant damselfly. The most similar extant damselfly is the neotropical platystictid *Palaemnema.* Therefore this specimen most likely is a curious stem-group representative of Platystictidae (the retained long vein CuA would then be a unique plesiomorphy), and thus the only putative fossil member of this family yet known.

(43-44) A nearly complete and beautifully preserved damselfly in Baltic amber was recently offered by the German amber trader Jens von Holt (Hamburg). According to Grimaldi (pers. comm. 1998) it may be purchased by the American Museum of Natural History (New York). A second amber damselfly for sale is currently present in the collection of another trader according to Holt (pers. comm. 1998).

(45) According to Grimaldi (pers. comm. 1998) an isolated wing of a dragonfly (!) in Baltic amber is present in the collection of the American Museum of Natural History in New York. This specimen seems to be the only existing Anisoptera from Baltic amber, since the present deposition of the only other specimen (in collection Menge) is unknown and this specimen might even be lost.

Odonates in cretaceous amber from Lebanon

(46) According to Nel (pers. comm. 1998) a wing fragment with some cells of an odonate in Lower Cretaceous amber from Lebanon (Lower Aptian, Hammana / Mdeirij, Casa Baada, Mouhafazit Jabal Libnen, Lebanon) is mentioned by Dejax & Masure & Azar (1996). This specimen is the only known fossil odonate in Cretaceous amber!

All these fossils together make a total of at least 46 different specimens that include only three adult dragonflies (Anisoptera) and only five larvae or rather exuviae. I know the present location of 35 specimens, of which 25 specimens are preserved in Germany, which therefore can be considered as real "El Dorado" for researches on amber odonates. This enumeration is probably still incomplete, since it is likely that some more specimens have disappeared in private collections without having been noticed by scientists. A few small damselflies are rumoured to be present in local collections in the Dominican Republic. Hagen (1856: 78) mentions the existence of an imaginal damselfly (collection Saturgus, Königsberg) and an odonate larva (Kabinett physik.-oekonom. Gesellschaft zu Königsberg), both from Baltic amber. However, these two specimens might be identical with specimens already mentioned in the present enumeration.

Most of the mentioned specimens are in need of a thorough revision, because their taxonomic and phylogenetic status is uncertain.

Acknowledgements

My sincere thanks are due to Mr Walter Ludwig (Berlin, Germany) for his invitation to study specimens in his private collection and for his kind loan of the holotype specimen of *Litheuphaea ludwigi* sp. n. and the new Saxonian specimen of *Platycnemis* ? *antiqua.*

I also owe many thanks to Dr Philip Perkins (MCZ, Cambridge, U.S.A.) for his kind support during my studies of the Carpenter collections at MCZ, to Dr Gerd Dietl and Dr Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart, Germany) for

providing a working place at the museum, to Dr André Nel (MNHN, Paris) for interesting discussions, to Dr Dieter Schlee (SMNS, Stuttgart), Dr George Poinar (Univ. California, Berkeley), and Dr David Grimaldi (AMNH, New York) for personal communications, and to Mrs Lynne Hambric (TAMU, U.S.A.) for information on the fate of the fossil collection of Dr O.M. Ball. Finally, I thank an anonymous reviewer for numerous suggestions.

This publication is part of the author's PhD thesis on the phylogeny of dragonflies at the Eberhard-Karls-University in Tübingen, and was supported from 1996-1998 by the "Graduiertenförderung" (LGraFöG) of the state Baden-Württemberg (Germany).

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