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Brief report

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A new dragonfly family from the Upper Cretaceous of France

ANDRE NEL, DIDIER NERAUDEAU, VINCENT PERRICHOT, VINCENT GIRARD, and BERNARD GOMEZ

The new aeshnopteran family Enigmaeshnidae is proposed for *Enigmaeshna deprei* gen. et sp. nov., the first fossil insect collected as imprint in the Earliest Cenomanian clay of the Puy-Puy quarry at Tonnay-Charente (Charente-Maritime, SW France). The bed bearing *E. deprei* was previously known for its highly diversified fossil plant assemblage. Although this taxon belongs to the much derived clade Aeshnodea, it is characterized by several unique hind wing venation characters, never found in other Aeshnoptera, viz. part of MAb distal of the trigonal planate very long, and presence of five posterior branches of AA directed towards posterior wing margin.

Introduction

Although Aeshnoptera are rather frequent in the Jurassic and Cretaceous fossil record, they almost all belong to the most inclusive clades of this group (Nel et al. 1994; Bechly et al. 2001). Mesozoic representatives of the Recent clade Neoaeshnida Bechly, 1996 are almost exclusively represented by the Gomphaeschnidae Tillyard and Fraser, 1940, sister group of the Aeshnodea Bechly, 1996. The few Mesozoic fossils of the latter clade belong to the family Allopetaliidae Cockerell, 1913 (genus *Baissaeshna* Pritykina, 1977). Little is known on the aeshnopteran history during the Late Cretaceous because of the lack of significant fossils. Thus, the present discovery of an Aeshnodea in the lowermost Cenomanian of France is of great interest in the knowledge of its diversity and morphological disparity during this crucial period of its evolution. The new fossil is characterized by several unique characters, allowing us to include it within a new family.

The fossil dragonfly comes from the Puy-Puy quarry, at Tonnay-Charente (Charente-Maritime, SW France), about 20 km from the Charente river estuary (Fig. 1). In this quarry, the uppermost Albian-lowermost Cenomanian deposits are transgressive and erosive on the Kimmeridgian substratum. These deposits are mainly composed of fluvial and paralic sand, but contain several clay intercalations with local concentrations of plant compressions or lignite and amber (Néraudeau et al. 2005). Stratigraphically (Fig. 2), the clay level containing fossil arthropod imprints is located about seven metres under the first facies clearly dated as Early Cenomanian, a marine shelly sand (lithological sub-unit B1) containing dense accumulation of the large benthic foraminifera *Orbitolina conica* (Vullo et al. 2003). The clay level bearing the fossil Aeshnodea corresponds to the base of the sand and clay alternations (lithological sub-unit A2), underlying the shelly sand. Just a few decimeters underneath the fossiliferous clay there is 2–3 m thick fluvial azoic sand arranged in large cross beddings (top of the sub-unit A1). The clay bearing arthropods and plants is devoid of sporomorphs and cannot be palaeontologically dated in this quarry (Peyrot et al. 2005). However, stratigraphical correlations with well-dated sections of other quarries from the same region (Néraudeau et al. 2002, in press), suggest an earliest Cenomanian age for the lithological sub-unit A2 from Puy-Puy.

The clay containing the fossil Aeshnodea corresponds to the basal part of the two main levels rich in plant compressions (P1, P2), as previously described by Gomez et al. (2004) and Néraudeau et al. (2005). Apart from numerous fossil ferns, conifers and angiosperms, the level P1 delivered a few imprints of undetermined Blattodea and decapod crustaceans. The Aeshnodea imprint was fossilized at a clay surface at a few centimeters of an 80-cm-l3ong *Dammarophyllum* leaf (Coniferale: Araucariaceae or Podocarpaceae).

Institutional abbreviation.—MNHN, Muséum national d'Histoire naturelle, Paris, France.

Other abbreviations.—AA anal vein; a.l., anal loop; AP anal posterior, A×0 A×1 A×2, primary antenodal cross-veins; CuAa, distal branch of cubitus anterior; CuAb, proximal branch of cubitus anterior; CuP, cubitus posterior; IR1 IR2, intercalary radial veins; MA, distal branch of median anterior; MAb, posterior branch of median anterior; MP, median posterior; Mspl, median supplementary; N, nodus; O, oblique vein; PsA, pseudoanal vein; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Rspl, radius supplementary; t.p., trigonal planate.

Systematic palaeontology

In the description below 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 in the present work, are based on the phylogenetic system proposed by Bechly (1996) and Bechly et al. (2001) for the Mesozoic Aeshnoptera.

Suborder Anisoptera Selys, 1854

Clade Aeshnoptera Bechly, 1996

Family Enigmaeshnidae nov.

Type genus: *Enigmaeshna* gen. nov., by monotypy.

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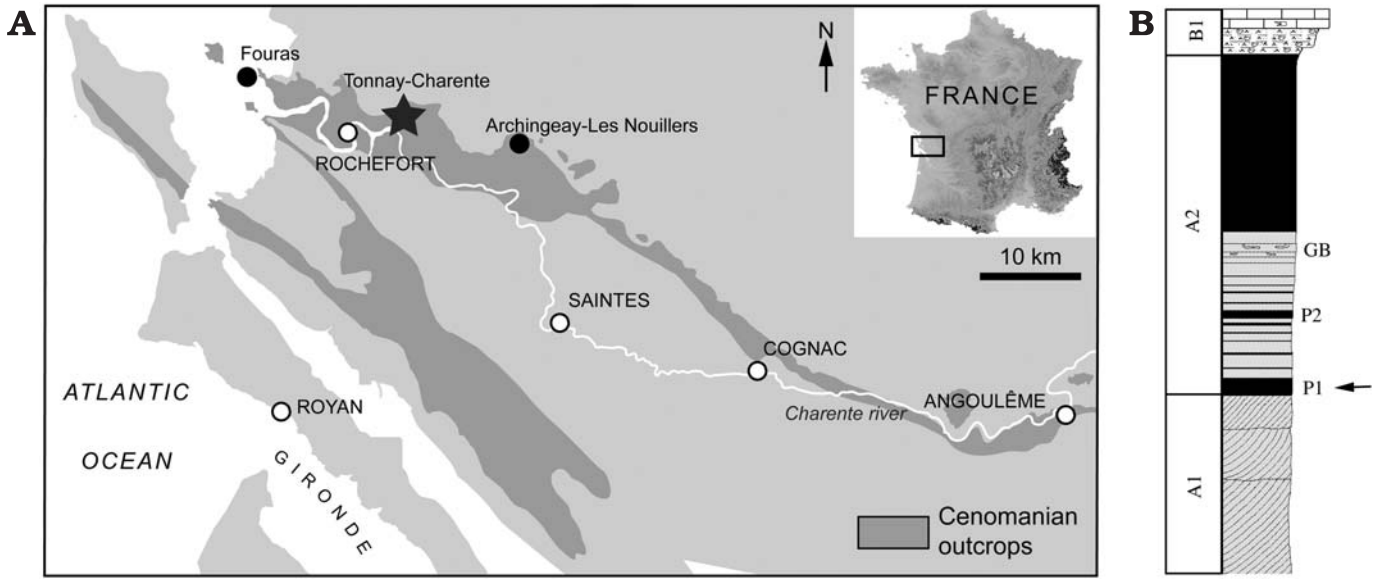


Fig. 1. Map of the Tonnay-Charente area (SW France) with location of the Puy-Puy quarry with Early Cenomanian deposits (**A**) and geological section (**B**) with the position of the studied sample with fossil Odonata (arrow). A1, fluvial sand with large cross beddings; A2, estuarine alternation of sand and clay, with three main fossiliferous levels (P1, plant compressions and arthropod imprints; P2, plant compressions only; GB, arthropods tracks); B1, marine shelly sand.

Diagnosis.—Hind wing characters only. Discoidal triangle divided into numerous cells, very elongate; part of MAb distal of the trigonal planate very long (autapomorphy); trigonal planate very strong and long (apomorphy); a long and straight pseudo-ScP distal of nodus (autapomorphy); submedian area and subdiscoidal space crossed by five cross-veins, with CuP and PsA not stronger than others; anal area very long, with five posterior branches of AA directed towards posterior wing margin (autapomorphy); anal loop broad, elongate, sub-rectangular, posteriorly closed, divided into numerous cells; one row of cells in area between MP and CuAa distal of discoidal triangle.

Genus *Enigmaeshna* nov.

Type species: *Enigmaeshna deprei* sp. nov.

Derivation of the name: Referred to genus *Aeshna* and the enigmatic position among Aeshnoptera.

Diagnosis.—As for the family.

Enigmaeshna deprei sp. nov.

Fig. 2.

Derivation of the name: After Eric Depré, who discovered the type specimen.

Holotype: MNHN-LP-R 63889, Eric Depré coll., imprint [female].

Type locality: Puy-Puy quarry, Tonnay-Charente, Charente-Maritime, France.

Type horizon: Late Cretaceous, Earliest Cenomanian, lithological subunit A2 (level P1 sensu Néraudeau et al. 2005).

Material.—Holotype only.

Diagnosis.—As for the family.

Description.—Print of basal half of a female hind wing, 29.6 mm long, wing 14.7 mm wide; distance from base to arculus 6.8 mm; from arculus to nodus 15.8 mm; from arculus to base of RP3/4 10.1 mm; no secondary antenodal cross-vein basal of A×1, six antenodal cross-veins of first row and five of second row between A×1 and A×2, 12 of first row and 9–10 of second row distal of A×2; distance from wing base to A×1 5.0 mm, between A×1 and A×2 6.1 mm; A×2 well distal of base of discoidal triangle; RP and MA strongly separated in arculus; hypertriangle 8.1 mm long, with seven cross-veins; discoidal triangle 1.8 mm distal of arculus, divided into eight smaller cells, very elongate and rather narrow, with basal side 2.3 mm long, anterior side 6.2 mm long, and MAb 5.7 mm long; a distinct angle in MAb at base of convex trigonal planate; part of MAb distal of trigonal planate very long, 2.5 mm long; postdiscoidal area with three rows of cells; a strong convex trigonal planate, long and nearly straight; only basal part of Mspl present, thus it is not possible to determine if it was well defined; a long and straight pseudo-ScP distal of nodus, four cells and 4.3 mm long; basal part of area between RA and RP with only five cross-veins basal of RP3/4, and five distal of base of RP3/4 and basal of subnodus; area between RP and MA with five cross-veins basal of RP3/4; one visible oblique vein "O" one cell distal of base of RP2; two rows of cells between IR2 and RP3/4 two cells distal of subnodus; one row of cells between MP and CuAa, with a strong narrowing of area between these veins opposite base of RP3/4; median area free; submedian area and subdiscoidal space crossed by five cross-veins, with CuP and PsA not stronger than others; posterior wing margin rounded at base (female specimen); anal area very long but not very broad, with five posterior branches of AA directed towards posterior wing margin, and 8–9 rows of cells between AA and posterior wing margin; anal loop rather broad, elongate, sub-rectangular, posteriorly closed, divided into nine cells; cubito-anal area broad, with 9–10 rows of cells between CuAa and posterior wing margin; CuAa with six posterior branches.

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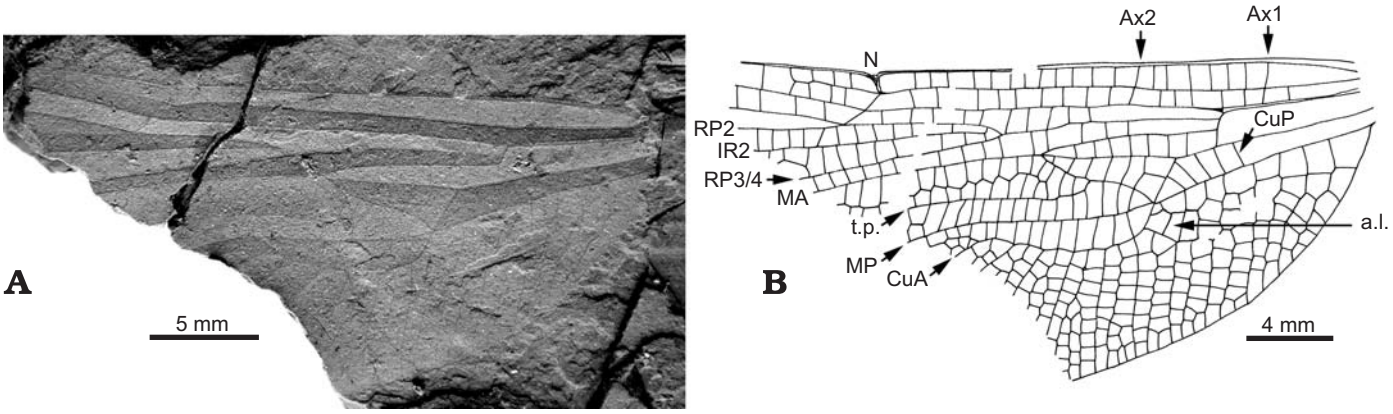


Fig. 2. Anisopteran *Enigmaeshna deprei* gen. et sp. nov. from Early Cenomanian of the Puy-Puy quarry (Tonnay-Charente, SW France). Holotype MNHN-LP-R 63889, photomicrograph (**A**) and explanatory drawing (**B**). Abbreviations: a.l., anal loop; A×1, A×2, primary antenodal cross-veins; CuAa, distal branch of cubitus anterior; CuP, cubitus posterior; IR2, intercalary radial vein; MA, median anterior; MP, median posterior; N, nodus; Pt, pterostigma; RP2, RP3/4, radius posterior; t.p., trigonal planate.

Discussion.—The very long discoidal triangle of this hind wing suggests affinities with the Aeshnoptera. The presence of a very strong convex trigonal planate is a specialized character convergently present in the gomphid genus *Hagenius* Selys, 1854 (and related taxa), the Mesozoic aeshnopteran family Liupanshaniidae Bechly, Nel, Martínez-Delclbs, Jarzembowski, Coram, Martill, Fleck, Escuillié, Wisshak, and Maisch, 2001 and the clade Neoaeshnida Bechly, 1996 (Bechly et al. 2001; Lin et al. 2002). However *Enigmaeshna* gen. nov. has not the main synapomorphies of the Liupanshaniidae, i.e., in hind wing, anterior side of discoidal triangle curved, and MAb strongly angular and sigmoidally curved. Furthermore, *Enigmaeshna* has a series of parallel cross-veins in its subdiscoidal space plus subdiscoidal triangle, including a weakened vein PsA of the same strength as other cross-veins, which is a character only present in the most advanced group Aeshnodea Bechly, 1996. However, within this clade, some taxa like *Brachytron* Evans, 1845 have retained a strong PsA. This character is sufficient to exclude affinities with the Liupanshaniidae and the Gomphaeschnidae, sister group of the Aeshnodea.

The presence of several accessory cubito-anal cross-veins is a potential synapomorphy of the Aeshnoidea Leach, 1815 (sensu Bechly 1996), and the presence of more than two rows of cells in the basal part of the postdiscoidal area would support affinities with the Aeshnidae Leach, 1815 (sensu Bechly 1996). Unfortunately, the lack of information on the structures of the distal half of this wing (Rspl, distal part of RP2, IR2, RP3/4, MA, Mspl, pterostigma), and the lack of the forewing impede us to be more precise on its affinities within the Aeshnodea. Nevertheless, *Enigmaeshna* differs from all the known Aeshnoptera in very important structures that allow us to consider that it does not belong to any of the known subclades of this group, viz. part of MAb distal of the base of the trigonal planate very long (more than length of three cells instead of 1–2 in other Aeshnoptera), and anal area very elongate with five posterior branches of AA basal of the anal loop. A further specialized character is the presence of a pseudo-ScP distal of the nodus, but it is also present in some Recent and Cenozoic Aeshnidae (*Aeschnophlebia* Selys, 1883).

Palaeoenvironmental discussion

Sedimentological and palaeontological characteristics of the fossiliferous clay of Puy-Puy indicate a coastal depositional environment with significant continental inputs (Néraudeau et al. 2005). First, sand and clay alternations of the sub-unit A2 (Fig. 2) are characteristic of an estuarine environment. The ripple marks and the arthropod tracks observed in the sandstones (GB in Fig. 1) overlying the insect-bearing clay are characteristic of a sandy tidal beach. The "azoic" sand with large cross beddings (sub-unit A1) preceding the clay with plants and arthropods is typical of a fluviatil series (Néraudeau et al. 2005). Moreover, a rich floristic assemblage is associated to the fossil arthropod imprints. Ferns, conifers, and angiosperms are highly diversified (more than thirty forms), and usually represent distinct taxa compared to other Late Albian and Early Cenomanian beds bearing plant compressions of the same region (Coiffard et al. 2004; Gomez et al. 2004; Le Diourion 2005; BG unpublished data). The particular high diversity and plant association of the P1/P2 beds at Puy-Puy quarry may correspond to freshwater marsh or pond in floodplain or mouth estuary. Fossil wood is relatively uncommon, with two identified taxa (*Agathoxylon* and *Podocarpoxylon*) (Perrichot 2005), but fossil leaf imprints are very abundant, with the outstanding abundance and diversity of angiosperms (e.g., *Myrtophyllum* cf. *angustum*), the presence of Araucariaceae or Podocarpaceae (e.g., *Dammarophyllum*), Cupressaceae–Taxodiaceae (e.g., *Glenrosa* sp.), other coniferales (e.g., *Geinitzia reichenbachii*), pteridophytes (e.g., cf. *Osmunda cretacea*), ginkgoales (e.g., *Nehvizdya andegavense*) (Le Diouron 2005; Néraudeau et al. 2005). Thus the life environment of *Enigmaeshna deprei* was probably an estuarine forest context combining a mosaic pattern of marine and fluvial influences.

Compared to the insect assemblages previously discovered in the Late Albian/Early Cenomanian ambers from the same region (Charente-Maritime, SW France) (Néraudeau et al. 2002, 2003; Perrichot 2005), the outcrop of Puy-Puy appears original and exciting because it is the first that contains clay with insect

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imprints. Moreover, contrasting with the about 1000 specimens of arthropods found regionally in amber, it is the first time that an Odonata is recorded in the mid Cretaceous deposits from Charentes. It can be assumed that further analyses of the fossiliferous clay of Puy-Puy will enrich the knowledge of the Albian–Cenomanian insects from France.

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