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Abstract

The discovery of the first damselfly *Lestes regina* from Monteils (Gard, France) supports the identity of late Eocene age of this outcrop with the historical outcrop of Célas, type locality for the type series of this species. *Lestes regina* is also documented from the late Eocene Isle of Wight basin, confirming the presence of significant contacts between this southern area and the anglo-Parisian lacustrine basin at that time. Nearly all the Eocene and Oligocene fossil *Lestes* from Western Europe have a particular character, viz. the presence of a supplementary row of cells between the veins MP and CuA. This character is much less frequent in extant *Lestes* and is still unknown among Neogene representatives of the genus.

Key words: Odonatoptera, late Eocene, Monteils Formation, paleobiogeography, wing venation.

Introduction

Even though the Lestoidea are recorded from the Lower Cretaceous with *Cretalestes martinae* Jarzembowski *et al*., 1998, the oldest accurate fossil record of the extant family Lestidae comes from the late Eocene, as the Paleocene *Lestes zalesskyi* Piton, 1940 is based on a poor and lost fossil of Zygoptera of uncertain position (Piton, 1940; Nel & Paicheler, 1994). The oldest known Lestidae have been found in the lacustrine outcrops of the Isles of Wight (UK) and Célas (France). The discovery of new Eocene fossils of this family can be of great interest. Here, we describe the first fossil Odonata found in the upper Eocene outcrop of Monteils (Gard, France). This outcrop is very rich in fossil plants, fishes and insects, although rather few of these have been described (Laurent, 1899, 1910; Feist-Castel, 1971; Nel, 1988; Séméria & Nel, 1990; Rückert-Ülkümen, 2001; Nel *et al*., 2008; Legalov, 2013; Perrard *et al*., 2014; Cai *et al*., 2014; Skartveit & Nel, 2017).

Material and method

The studied specimen was collected from the yellowish late Eocene (Priabonian) shale of Alès-Monteils in Gard, southern France (44°05′9″N, 04°11′39″E, after the BRGM geological maps 1/50 000, numbers 912 – Alès, XXVIII – 40 and 938 - Anduze, XXVIII-41). It was examined using a Leica M300 binocular and photographed using a Nikon D5100 camera equipped with a Nikon AF 60 mm Micro lense.

We follow the wing venation nomenclature of Riek & Kukalová-Peck (1984), modified by Nel *et al*. (1993), Bechly (1996, 2016) and Jacquelin *et al*. (2018).

Abbreviations. Ax, primary antenodal crossvein; arc, arculus; dc, discoidal cell; sn, subnodus; C, Costa; Pt, pterostigma; RA, Radius anterior; RP, Radius posterior; IR, Interradius; MA, Media anterior; MP, Media posterior; CuA, Cubitus anterior. Add: N, nodus, which has indicated in the Fig.2.

Systematic paleontology

Order Odonata Fabricius, 1793

Family Lestidae Calvert, 1901

Genus *Lestes* Leach, 1815

Lestes regina Théobald, 1937

(Figs 1–2)

Material. Specimen UBGD 32320 (imprint, a nearly complete damselfly with all legs and wings preserved, sex unknown), stored at the Université de Bourgogne, Géologie, Dijon, France; counterimprint in Coll. Benjamin Latutrie.

Description. Body black, wings hyaline with pterostigma dark brown. Head deformed as in all fossil Lestidae, with mouthparts anteriorly projected, 2.6 mm long, and 3.5 mm wide. Thorax 6.0 mm long, and 3.4 mm wide. Fore- and hindwing nearly identical, in particular discoidal cells of same shapes and widths; fore wing 19.9 mm long, 4.5 mm wide, ratio L/W 4.4, width at nodus level 3.2 mm; pterostigma 2.3 mm long, and 0.5 mm wide; distance from base to arculus 3.7 mm, from arculus to nodus 3.7 mm, from nodus to pterostigma 9.8 mm, and from subnodus to base of RP2 2.8 mm; oblique vein ‘O’ two cells distal of base of RP2; a supplementary row of 5-6 cells between MP and CuA. Abdomen 27.9 mm long, 1.3 mm wide; cerci present but poorly preserved.

Discussion

The wing venation of this fossil is characteristic of the Lestidae and more precisely of the genus *Lestes*: long pterostigmata; bases of RP3/4 and IR2 midway between arculus and nodus; an oblique crossvein ‘O’; distal discoidal vein MAb very oblique, with distal angle of discoidal cell very acute; MA strongly zigzagged; area between IR2 and RP3/4 distally strongly widened

with three rows of cells between these two veins; fore- and hindwing discoidal cells of the same width and shape. One species of this genus was already described from the uppermost Eocene of Célas (in a lost outcrop at the old trench at the entrance to an abandoned railway tunnel), an outcrop situated at 4 km to and contemporaneous with Monteils (Cavelier, 1979), viz. *Lestes regina* Théobald, 1937. The holotype of this species is probably lost and Nel & Paicheler (1994: 10-11, fig. 5) designated a lectotype and redescribed it. Mentioned below are the very few differences between *L. regina* and the herein described specimen.

The fore wing of the specimen from Monteils is 19.9 mm long, 4.5 mm wide, ratio L/W 4.4, width at nodus level 3.2 mm; while in the holotype of *Lestes regina*, the fore wing is 21.5 mm long, 4.6 mm wide with a ratio L/W 4.7 (Théobald, 1937). In the lectotype, the fore wing is 22.0 mm long, 4.5 mm wide with a ratio L/W 4.8, width at nodus level 3.0 mm (Nel & Paicheler, 1994). The body dimensions are less reliable because of possible deformations due to taphonomic processes. Nevertheless, the abdomen is shorter than in the holotype of *L. regina* (27.9 mm long vs. 33.0 mm), and broader (1.3 mm vs. 0.75 mm). An additional difference could be the presence of three cells between base of RP2 and oblique vein 'O' in the lectotype of *L. regina*, whereas there are only two in the specimen from Monteils. In our opinion, the aforementioned differences are not sufficient to clearly separate this latter from *Lestes regina*. This discovery confirms that the two outcrops of Célas and Monteils are contemporaneous or nearly so, despite the different sediment aspect between them (darker limestone at Célas, compared to the white to grey blue limestones at Monteils).

Conclusion

The occurrence of *Lestes regina* in the three localities of Célas, Monteils and Isle of Wight suggests that there were significant contacts between the region of Alès and the northern Anglo-Parisian lacustrine basin. Feist-Castel (1971) came to the same conclusion based on

charophytes. The presence of the same genus of Orthoptera Tettigoniidae at Célas and at Isle of Wight further strengthens this hypothesis (Nel *et al*., 2008).

The presence of a supplementary row of cells between MP and CuA is encountered in several Eocene-Oligocene *Lestes* spp. from Europe, viz. *Lestes regina*, *Lestes* aff. *regina* (late Eocene, Isles of Wight, UK, Nel and Fleck, 2014), *L. ceresti* Nel & Papazian, 1985, *Lestes brisaci* Nel *et al*., 1997 (both from the late Oligocene, France), *L. statzi* Schmidt, 1958 (late Oligocene, Germany), *L. foersteri* Hess, 1895 (early Oligocene, France), and *L. aquisextanus* Nel, 1985 (latest Oligocene, France) (Hess, 1895; Schmidt, 1958; Nel, 1985; Nel & Papazian, 1985; Nel *et al*., 1997). The two lestid species of uncertain generic affinities *Lestes vicina* Hagen, 1858 (early Oligocene, Germany) and *Lestes plicata* Piton & Théobald, 1939 (early Oligocene, France) also have this supplementary row of cells (Hagen, 1858; Piton & Théobald, 1939; Nel & Paicheler, 1994). Conversely, the Miocene European species of *Lestes* do not exhibit this particular character. Compte-Sart (2014) indicated that this supplementary row of cells between MP and CuA can be found also in some specimens but not in others, of extant *Lestes* species (*L. dryas*), and therefore considered it of minor importance. Yet, it would be somewhat significant to find it in all specimens of *L. ceresti* and *L. regina*. Naturally, these fossils are still too few (ca. 10 specimens of *L. ceresti*) to represent a valid statistical basis. More specimens are necessary to draw any conclusion on the frequency and stability of this character among the Eocene-Oligocene species of *Lestes*. Nevertheless, it seems that this character was more frequent among the Paleogene *Lestes* than in the Neogene ones.

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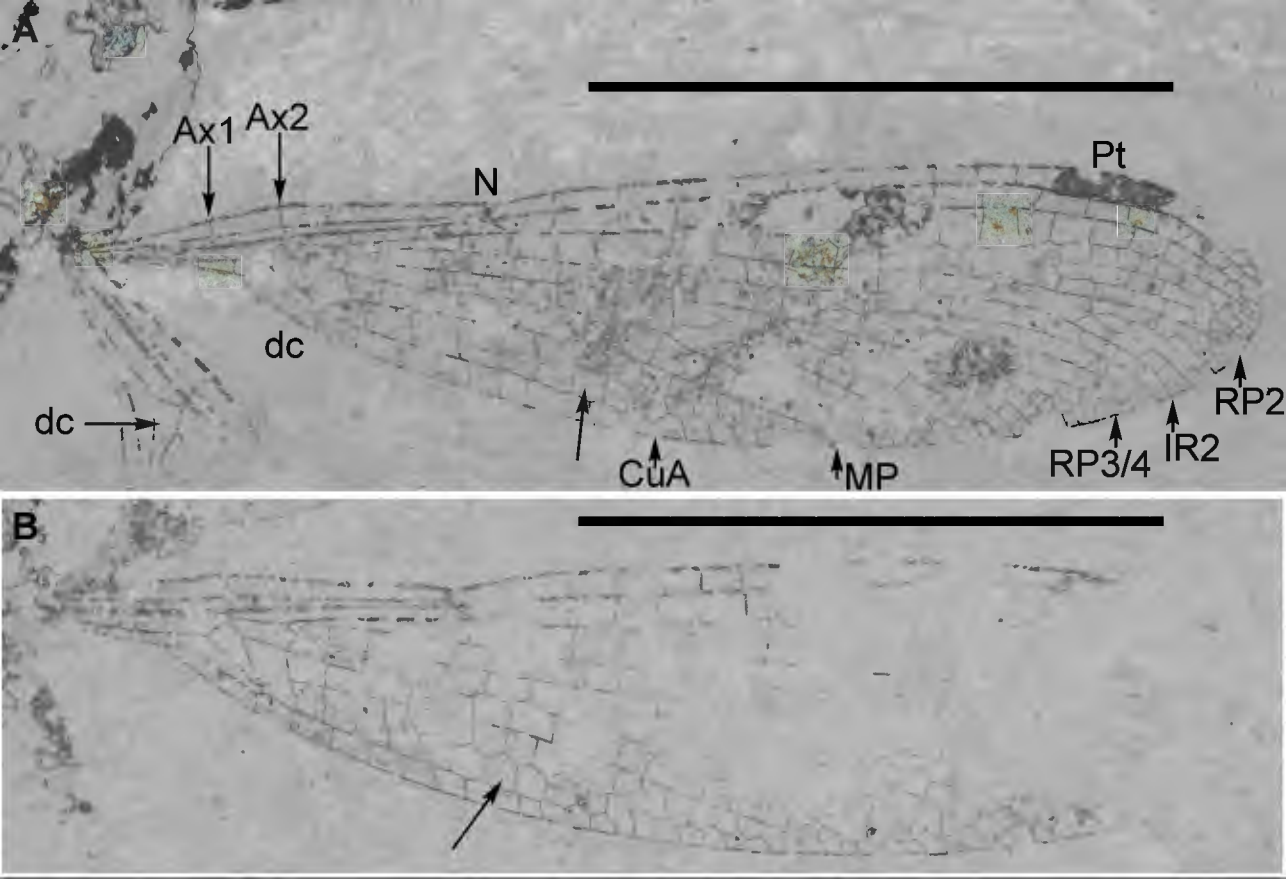
FIGURE 1. *Lestes regina* Théobald, 1937, UBGD 32320, Monteils. General habitus. Scale bar = 10 mm.

FIGURE 2. *Lestes regina* Théobald, 1937, UBGD 32320, Monteils. (A) Fore wing; (B) Hindwing, arrow supplementary row of cells between MP and CuA. Scale bar = 10 mm.


A
Ax1
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N
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MP
RP3/4
IR2
RP2
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