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Historical Biology

The second oldest representative of the genus *Aeshna* (Odonata: Aeshnidae) found in the Lowermost Oligocene of Luberon (France) and revealed by UV light

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ABSTRACT

Aeshna caseneuvensis sp. nov., second oldest representative of the genus *Aeshna*, is described and figured from the Lowermost Oligocene of Luberon in southeastern France. The oldest

described species in this genus is from the Uppermost Eocene of Colorado in USA. Their occurrence in very distant areas in an interval of time of less of five millions years strongly suggests that the genus is older, possibly appearing during the middle Eocene, as it is still unknown in the early Eocene odonate faunas. The specimen could be studied thanks to a technique of photograph under UV light newly developed by one of us (RG).

KEYWORDS

Insecta; Odonata; Aeshnoptera; Aeshnini; sp. nov., Earliest Oligocene; UV light photographs of fossil insects

Introduction

The hawker dragonflies or Aeshnidae are well-known flying predators of large size, present over nearly the continents except Antarctica. Their stem group Aeshnoptera are among the oldest Anisoptera, being already diverse during the Middle Jurassic (Bechly et al. 2001; Zheng 2021), but the Aeshnidae sensu stricto (excluding the Gomphaeschnidae) are still only known in the Cenozoic. They are rather frequent as compression fossils during the Eocene, Oligocene, and Miocene (e.g., Nel *et al*. 1994, 1996; 1997; Nel and Petrulevičius 2010; Archibald and Cannings 2019, 2022), but they remain nearly unknown in the Paleocene (Garrouste and Nel 2019). Several early Eocene representatives of the subfamily Aeshninae are known (see list in Archibald and Cannings 2019), but the oldest record of the tribe Aeshnini and genus *Aeshna* Fabricius, 1775 is from the uppermost Eocene of USA (Scudder 1890). Here we describe a second representative of the genus *Aeshna* from the lowermost Oligocene of France, suggesting that this genus is much older and was already quite widespread during the latest Eocene.

Material and methods

The fossil has been discovered by one of us (PC), in rocks fallen from a newly discovered outcrop in the high cliffs of Haute Blace - Pantalliane near Caseneuve at the Doghead Locality, together with numerous plant remains (leaves, seeds, flowers), abundant freshwater Isopoda, and few Diptera, mainly Bibionidae of the genus *Plecia*. These layers were previously known from the cliffs near Barbeiras, an outcrop also close to Caseneuve, in which some *Prolebias* fish specimens, a large wing of Trichoptera, a winged Formicidae, few Heteroptera Pentatomidae, an adult Culicidae, numerous chironomid adults and larvae and numerous adult *Plecia* (Bibionidae) were also found by one of us (AN) more than twenty years ago. The fossiliferous deposits of Haute Blace - Pantalliane and Barbeiras belong to the Calcaire de La Fayette Formation. This geological unit is mostly made of limestones, marls and evaporites deposited in a closed lacustrine basin that once encompassed a ca. 10x30 km^2 area centered over the city of Apt (Lesueur 1991). The thin layers yielding fossil insects are papyraceous limestones situated in the basal part of the formation interpreted as produced by bacterial mats in the shallow parts of a lacustrine ramp in quiet hydrodynamic conditions (Lesueur 1991). The Calcaire de La Fayette Formation is dated to the early Rupelian (mammalian biohorizon MP21) based on studies of gastropod molluscs, charophytes, ostracods, and vertebrate tracks (Feist 1977; Cavelier et al. 1984; Apostolescu and Guernet 1992). It is older than the nearby Campagne-Calavon Formation, which has yielded the well-known Céreste paleobiota dated as Rupelian (biohorizons MP23–24) with several fossil Odonata, including some Aeshnidae. The most significant difference between the MP21 and MP23-24 paleolakes is the complete absence of freshwater Isopoda in the later lake (Campagne-Calavon Formation), while they are abundant in the earlier paleolake (Calcaire de La Fayette Formation). Also, the *Prolebias* species from the Doghead locality is different from the species found at the later site in Céreste, after a personal communication of the late Jean Gaudant who studied the fish specimens from the area but never published them. These fossiliferous sites are protected by the Luberon national

geologic nature Reserve (Coster and Legal 2021). The concerned cliffs are also extremely dangerous because of falling stones.

The specimen was examined with a Nikon SMZ 25 stereomicroscope and photographed with a Canon 50D with an attached Canon 65 MPE camera lens and mounted on an automated stacking rail (StackShot). All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software. The specimen was also photographed at CEREGE using a Camera Sony Alpha 7R IV (61.2MP, Full frame, Pixel Dimensions, 9504 x 6336) with a Zeiss Macro 90mm lens and dual Flash lighting. Pictures were recorded in RAW format for further post-processing. Colors have been calibrated with X-Rite ColorChecker ® Classic chart and ColorChecker Passport software. Raw photo development and editing for white balance, colors, and aberrations made with Capture One 20 software. Other photographs with normal light were taken using a Nikon SMZ 25 microscope with a Nikon Z7II camera. UV light photographs were taken with Nikon D850 FX camera with a 60 mm/2.8 Micro-Nikkor. UV light (365 nm) have been used to find differential chemical composition with different visible fluorescence contrast with sedimentary matrix and revealed putative ornamentations or patterns on the wing surface. High definition images (45 MP sensor) permitted cropping into images. UVA (365 nm rather than 390 nm) use for fossil insect studies is a new useful and promising technique for enhancing observation with a simple, portable and economic device. It is a useful way to select specimens of interest for chemical analysis and imaging by more sophisticated techniques (e.g., X-ray synchrotron fluorescence, Georgiou et al. 2019).

We follow the wing venation terminology of Riek and Kukalová-Peck (1984), as modified by Jacquelin et al. (2018). For the basal classification of the Aeshnoptera, we follow Bechly (1996), Bechly *et al.* (2001), and Ellenrieder (2002) for the classification of the extant

Aeshnidae. Vein abbreviations are: a.l. anal loop; Ax1 and Ax2 primary antenodal crossveins; Bqs crossveins between RP1/2, IR2 and 'O'; C costal vein; CuA cubitus anterior; CuAa anterior branch of CuA; d. discoidal triangle; CuP cubitus posterior; IR1 and IR2 intercalary radial veins; N nodus; MA media anterior; MAa anterior branch of MA; MP media posterior; 'O' oblique vein between RP2 and IR2; Pt pterostigma; RA radius anterior; RP radius posterior; Rspl and Mspl supplementary radial and median veins; ScP subcostal posterior.

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Results

Order: Odonata Fabricius, 1793

Family: Aeshnidae Leach, 1815

Genus: *Aeshna* Fabricius, 1775

***Aeshna caseneuvensis* sp. nov.**

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(Figures 1–4)

Holotype

PNRL 2714 (part and counterpart of a head with thorax with parts of the four wings attached), stored in the Musée of Geology, Parc naturel regional du Luberon, Apt, France.

Type locality

Cliff of Haute Blace - Pantalliane near Caseneuve Village, Vaucluse, Luberon, France.

Type stratum

Earliest Oligocene, Formation of 'Calcaires de La Fayette' (MP21),

Etymology

Named after the type locality Caseneuve.

Diagnosis

Wing character only. Fork of IR2 well-defined, well basad pterostigma; area between Rspl and IR2 with four rows of cells in-between; four rows of cells in area between Mspl and MAa; anal loop with 10 cells in three rows; discoidal triangles with seven cells.

Description

Body and wings without trace of coloration; head compressed and poorly preserved, 5.2 mm long, 7.4 mm wide; thorax 14.4 mm long, 7.0 mm wide; wings probably hyaline; forewings ca. 48.9 mm long, ca. 11.5 mm wide, distance between base and arculus 6.7 mm, between arculus and nodus 12.6 mm; pterostigma elongate, 4.7 mm long, 1.0 mm wide, with basal and distal sides strongly oblique, covering three cells; pterostigmal brace present, aligned with basal margin of pterostigma, and strongly oblique; two primary antenodal crossveins Ax1 basad arculus and Ax2 opposite middle of discoidal triangle, with three secondary crossveins in-between, between C and ScP; 15 antenodal crossveins distad Ax2; ca. 15 postnodal crossveins; median space free; ca. five crossveins in submedian-subdiscoidal area; arculus between Ax1 and Ax2, slightly closer to Ax1; RP and MA nearly meeting at their base in arculus; posterior part of arculus not aligned with anterior part; hypertriangle crossed by five veins, 8.4 mm long, 0.7 mm wide; discoidal triangle elongate but narrow, 7.1 mm long (costal side), 2.5 mm wide (proximal side), subdivided into seven cells; posterior side 6.6 mm, angled; convex trigonal planate in postdiscoidal area rather well-defined but short; Mspl long, with a strong concave bend, and with four rows of cells between it and MAa; MA, and RP3/4 not parallel in their distal part, and MA with a strong concave bend before wing margin; two rows of cells between MA, and RP3/4; base of RP3/4 between nodus and arculus; base of RP2 aligned with subnodus; oblique vein ‘O’ one cell distad base of RP2; distal fork of I R2 symmetrical, three cells, 3.8 mm basad level of pterostigma, with three rows of cells in area between its branches; RP2

parallel with anterior branch of IR2, making a distinct but smooth curve; one row of cells between RP2 and anterior branch of IR2; base of IR1 below pterostigma; Rspl distinctly curved, with four rows of cells between it and lR2; hind wings incompletely preserved, ca. 48 mm long, ca. 15.5 mm wide, distance between base and arculus 6.7 mm, between arculus and nodus 14.4 mm; discoidal triangle shorter and broader than that of forewing, 6.7 mm long (costal side), 2.6 mm wide (proximal side), posterior side 5.4 mm, pterostigma incompletely preserved; venation nearly identical to that of forewing, except in the cubito-anal area; anal angle not preserved; anal loop closed, well-defined, broad and large, 3.8 mm long, 6.5 mm wide, divided into 10 cells; one row of cells between MP and CuA between their base and nodus level; CuAa with five posterior branches that define groups of cells, and ca. six rows of cells between it and posterior wing margin.

Remark

While the fossil is hardly visible under normal light, photographs under ultraviolet light were extremely efficient to show all the available body and wing venation details (see Figs xxxx). This new approach is very interesting for the study of fossil insects, rendering details of venation, color patterns, etc.

Discussion

This fossil has all the autapomorphies of the family Aeshnidae as defined by Bechly (1996), i.e. 'aeshnid bulla' in distal part of MA in both pairs of wings; subdiscoidal triangle of both wings crossed by one crossvein; Rspl and Mspl distinctly curved with more than one row of cells between them and IR2 or MA, and area in between divided by oblique intercalary veins; more than two rows of cells in basal part of postdiscoidal area between level of distal angle of discoidal triangle and level of midfork; and hypertriangle traversed by at least three crossveins in forewings. After Ellenrieder (2002), this fossil fits into the clade 'Aeshnini' for the following

synapomorphies: more than one cubito-anal crossvein; IR2 fork present; RP2 evenly curved; MA and RP3/4 not parallel, MA with a concave bend before wing margin; Mspl with a concave bend at distal portion; Rspl not parallel to IR2, with a concave bend. The RP2 without marked convex bend at proximal end of pterostigma, is a plesiomorphic character state that would exclude affinities with the group (*Anaciaeschna* Selys, 1878 – *A. isosceles* – *Andaeschna* De Marmels, 1994 – *Anax* Leach, 1815 – *Hemianax* Selys, 1883), plus the fossil genus *Merlax* Prokop and Nel, 2000, although we do not have apomorphies to support an attribution to one of the other genera of Aeshnini, i.e. *Castoraeschna* Calvert, 1952, *Coryphaeschna* Williamson, 1903, *Remartinia* Navás, 1911, *Oreaeschna* Lieftinck, 1937, and *Aeshna* Fabricius, 1775. Nevertheless, both this fossil and *Aeshna* differ from *Castoraeschna*, *Oreaeschna*, *Coryphaeschna*, and *Remartinia* in the broad area between the branches of IR2, and forking of IR2 well basad pterostigma.

Among the fossil species with a distinctly forked IR2 currently put in the genus *Aeshna*, the new fossil differs from the early Miocene *Aeshna zlatkokvaceki* Prokop et al., 2016 and the latest Oligocene *Aeshna oligocenica* Nel et al., 1994 in the fork of IR2 well basad the pterostigma vs. just basad it (Nel et al. 1994; Prokop et al. 2016). The latter also has a broader area between Rspl and IR2 with six-seven rows of cells in-between. The late Miocene *Aeshna cerdanica* Nel and Martínez-Delclòs (in Nel et al. 1994) is much smaller than the new fossil, with a larger area between Rspl and IR2 and a smaller anal loop with nine cells vs. 10. The late Miocene *Aeshna andancensis* Nel and Brisac (in Nel et al. 1994) also has a smaller anal loop with eight cells disposed in two rows. The late Miocene *Aeshna multicellulata* Gentilini and Peters, 1993 has a quite broader area between Rspl and IR2 and the fork of IR2 opposite the base of the pterostigma. *Aeshna messiniana* Gentilini and Peters, 1993, *Aeshna ghiandonii* Gentilini and Peters, 1993, and *Aeshna turoliana* Riou and Nel, 1995 have the fork of IR2 just basad the base of the pterostigma (Gentilini and Peters 1993; Riou and Nel 1995). The Middle

Miocene *Aeshna stavropolensis* Nel et al., 2005 and *Aeshna shanwangensis* Li et al., 2011 have a larger anal loop and a broader area between Rspl and IR2 than the new fossil (Nel et al. 2005; Li et al. 2011). *Aeshna forficatum* Li et al., 2011 also has a broader area between Rspl and IR2. On the contrary *Aeshna ignivora* Zhang, 1989 has a narrower area between Mspl and MAa and discoidal triangles with only five cells vs. seven in the new fossil (Zhang 1989). The late Miocene *Aeshna vösendorfensis* Papp and Mandl, 1951 is too incomplete to be compared to the new fossil. It seems to differ from it in the narrow space between MP and CuA near posterior wing margin (Papp and Mandl 1951: fig 1). The 'cf. *Aeshna* sp.' described by Prokop et al. (2016), based on an incomplete forewing, differs from the new fossil in the presence of only three rows of cells in areas between Mspl and MAa and between Rspl and IR2. The Latest Eocene *Aeshna solida* Scudder, 1890 has smaller wings, 44 mm long vs. more than 45 mm, and has a forewing discoidal triangle subdivided into five cells instead of seven in the new fossil (Scudder 1890). *Aeshna ollivieri* Nel, 1986 from the Oligocene of Céreste (Luberon) and the '*Aeshna* sp. *incertae sedis'* described by Martínez-Delclòs and Nel (1991), have a rudimentary fork of IR2 (Nel 1986).

Conclusion

The oldest known representative of the genus *Aeshna* is *A. solida* from the Uppermost Eocene (Priabonian, Chadronian, 37.2 - 33.9 Ma, MP19) of Florissant (Colorado, USA) (Nel et al. 1994). Thus *Aeshna caseneuvensis* sp. nov. from the mammal level MP21 (earliest Oligocene, Rupelian) is the second oldest representative of this genus. Their presence in localities situated in Central North America and Western Europe strongly suggests that the genus is much older, even if some odonatofaunal exchanges occurred during the Eocene between these two areas (Garrouste and Nel 2019). No representative of the Aeshnini has yet been described from the

Lower Eocene aeshnid fauna of North America (Archibald and Cannings 2019). The present discovery will be very useful for future calibrations of the aeshnid phylogeny.

The entomofauna of the Calcaire de La Fayette Formation is dominated by the bibionid genus *Plecia*, while the genus *Bibio* was not recovered. This suggests a warmer paleoclimate than for Céreste, in which *Bibio* is well represented even if less diverse and abundant than *Plecia* (Collomb et al. 2008; Skartveit and Nel 2017). Possibly, the diversification of the genus *Aeshna* during the Oligocene and Miocene could be related to the cooling that occurred at these times.

Acknowledgements

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Figure 1. *Aeshna caseneuvensis* **sp. nov**., holotype PNRL 2714. Photograph of part under normal light.

Figure 2. *Aeshna caseneuvensis* **sp. nov**., holotype PNRL 2714. Photograph of counterpart under UV light. Scale bar = 5 mm.

Figure 3. *Aeshna caseneuvensis* **sp. nov**., holotype PNRL 2714. Photograph of hind wing basal half under UV light, al anal loop, d discoidal triangle. Scale bar = 5 mm.

Figure 4. *Aeshna caseneuvensis* **sp. nov**., holotype PNRL 2714. Photograph of hind wing under UV light, al anal loop, d discoidal triangle. Scale bar = 5 mm.

figure 1

179x203mm (300 x 300 DPI)

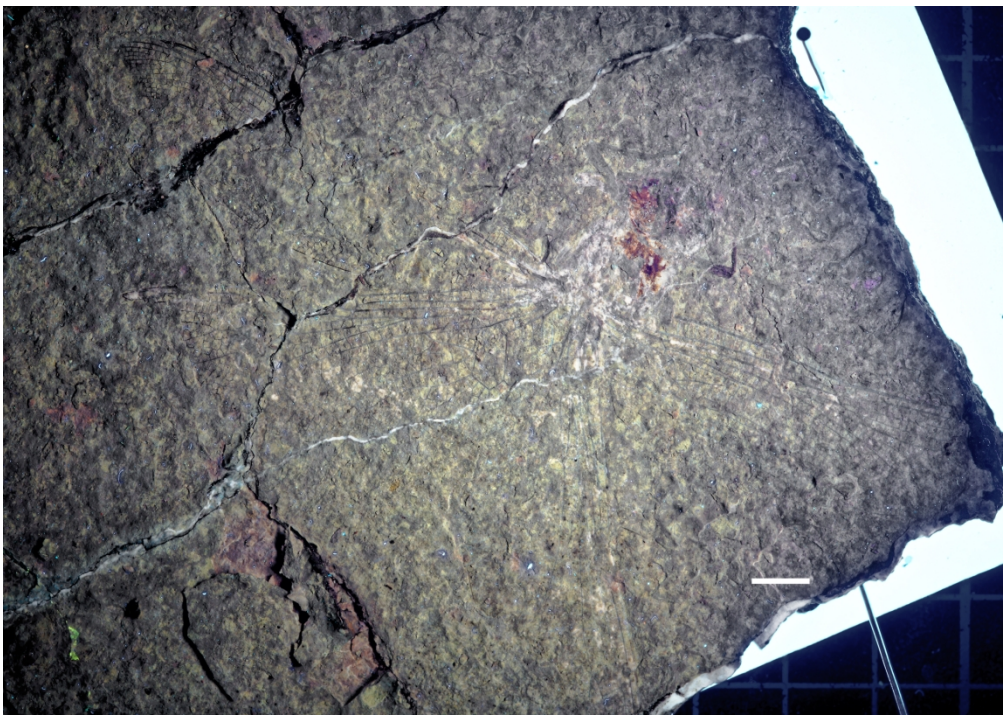

figure 2

180x127mm (300 x 300 DPI)

figure 3

180x110mm (300 x 300 DPI)

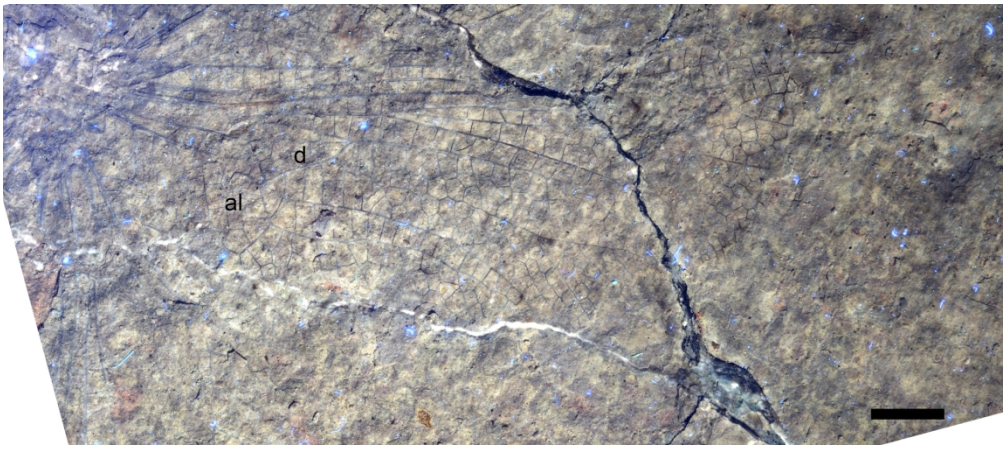

figure 4

180x79mm (300 x 300 DPI)