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ABSTRACT
A new malachite damselfly, *Palaeophylolestes distinctus* n. gen., n. sp., is described from the Paleocene Menat locality. It can be distinguished from other Synlestidae owing to the very long wing veins MA, MP and CuA, and a unique combination of other wing venation features. The occurrence of a Synlestidae in the western Palaearctic area (while extant species occur in Australia, the Oriental region, South-East Asia, South Africa and Hispaniola) is not unexpected given the known fossil record of these insects and climatic conditions prevailing at Menat during the Paleocene.

KEY WORDS
Paleocene,
Menat,
France,
fossil insect,
new genus,
new species.

RÉSUMÉ
Palaeophylolestes distinctus *n. gen., n. sp., un nouvelle demoiselle malachite (Odonata: Zygoptera: Synlestidae) de la localité paléocène de Menat (France).*
Une nouvelle demoiselle malachite, *Palaeophylolestes distinctus* n. gen., n. sp., est décrite de la localité Paléocène de Menat. Elle se distingue des autres Synlestidae par des nervures alaires MA, MP et CuA très longues et une unique combinaison de traits de nervation alaire. L'occurrence d'un Synlestidae dans la zone Paléarctique occidentale (tandis que les espèces actuelles sont présentes en Australie, dans la région orientale, en Asie du sud-est, en Afrique du Sud et en Hispaniola) n'est pas inattendue considérant le registre fossile connu de ces insectes et les conditions climatiques régnant à Menat au Paléocène.

MOTS CLÉS
Paléocène,
Menat,
France,
insecte fossile
genre nouveau,
espèce nouvelle.

INTRODUCTION

The Menat locality is one of the few European localities documenting a Paleocene terrestrial environment, with a rich fossil material of vertebrates, plants and insects (Wedmann *et al.* 2018; and references therein). Among the latter, relatives of dragon- and damselflies are unexpectedly rare, with a total of 7 known species (Nel & Jouault 2022; and reference therein). New discoveries are therefore relevant to our understanding of the palaeogeographic distribution of these insects at the onset of the Cenozoic. In the following we describe a new specimen from the Menat locality pertaining to malachite damselflies (Synlestidae), a group currently distributed in Australia, the Oriental region, South-East Asia, South Africa and Hispaniola (Garrison *et al.* 2010; Kalkman *et al.* 2008; Simaika *et al.* 2020), but with a wider distribution in the fossil record (Petrulevičius 2018; and references therein).

MATERIAL AND METHODS

Fossil specimen

The studied specimen consists of a single slab housed at the 'Musée de Paléontologie de Menat', Menat, Puy-de-Dôme, France. The fossil is preserved flat, making it impossible to identify right and left wings. We therefore use an ad hoc terminology, with wings located on the left side of the body indicated as 'FW1' (for the forewing) and 'HW1' (for the hindwing; and, accordingly, 'FW2' and 'HW2' for those on the right side).

Wing venation homologies and terminology

Within the framework of the serial insect wing venation ground-plan (Lameere 1922, 1923), we follow topographic homology conjectures proposed by Riek & Kukalová-Peck (1984; and see Bechly, 1996) for total-Odonata. The following adopted terminology is repeated for convenience.

Abbreviations

AA	anterior Analis;
CuA	anterior Cubitus;
CuP	posterior Cubitus;
Irp_1-rp_2	intercalary vein between RP1 and RP2
Irp_{1+2}-rp_{3+4}	intercalary vein between RP1+2 and RP3+4
MA	anterior Media;
MP	posterior Media;
RA	anterior Radius;
RP1	anterior-most branch of RP1+2;
RP2	posterior-most branch of RP1+2;
RP1+2	anterior-most branch of the posterior Radius;
RP3+4	posterior-most branch of the posterior Radius;
ScP	posterior Subcosta.

Colour-coding

blue	radial system;
red	median system ;
green	cubital system ;
yellow	intercalary veins of the radial system;
purple	R+MA (or RA+(RP+MA));
light blue	cell below sub-discoidal (i.e. sub-quadrangular) cell.

Data acquisition

Photographs were taken using a digital camera Canon EOS 5D Mark III coupled to a Canon MP-E 65 mm macro lens (all Canon, Tokyo, Japan) equipped with a polarizing filter. The embedding rock was used as reference for white balance. The resulting photographs were optimised using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, United States).

Hand-made draft drawings were produced with the aid of a microscope equipped with a camera lucida (Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10×/23 eye pieces, a Plan Apo S 1.0× FWD objective; all Zeiss, Jena, Germany). Drawings were completed using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, United States) using both hand-made draft drawings and photographs. On Fig. 2, faded vein sections were reconstructed.

SYSTEMATIC PALAEONTOLOGY

Order ODONATA Fabricius, 1793
Suborder ZYGOPTERA Selys Longchamps, 1854
Family Synlestidae Tillyard, 1917

Genus *Palaeophylolestes* n. gen.

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Type species. — *Palaeophylolestes distinctus* n. sp.; monotypic genus.

Etymology. — After the name of a closely-related genus, namely *Phylolestes*, associated with the prefix 'Palaeo-', referring to the Palaeocene age of the type-species; gender masculine.

Diagnosis. — As for the type species.

Palaeophylolestes distinctus n. gen., n. sp.
(Figs 1; 2)

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Holotype. — BDL 2002, Musée de Paléontologie de Menat, Menat, Puy-de-Dôme, France.

Etymology. — The species epithet refers to the length of MA, MP and CuA, distinctly long in the species.

Type locality and stratigraphy. — Bord du Lac des Grelins (BDL), Menat, Puy-de-Dôme, France; middle Paleocene, Menat Basin.

Commented diagnosis. — Wings: RP1+2 / RP3+4 fork closer to nodus than to arculus (within Lestoidea, apomorphic for Synlestidae and Perilestidae); MA, MP and CuA reaching posterior wing margin very distally (unique to the species); forewing quadrangle with proximal edge about half length of posterior edge; cell below sub-discoidal (i.e. sub-quadrangular) cell well-developed, longer than sub-discoidal cell (plesiomorphy within Zygoptera; as opposed to 'cell reduced, with AA (or CuP+AA) diverging from posterior wing margin in distal position').

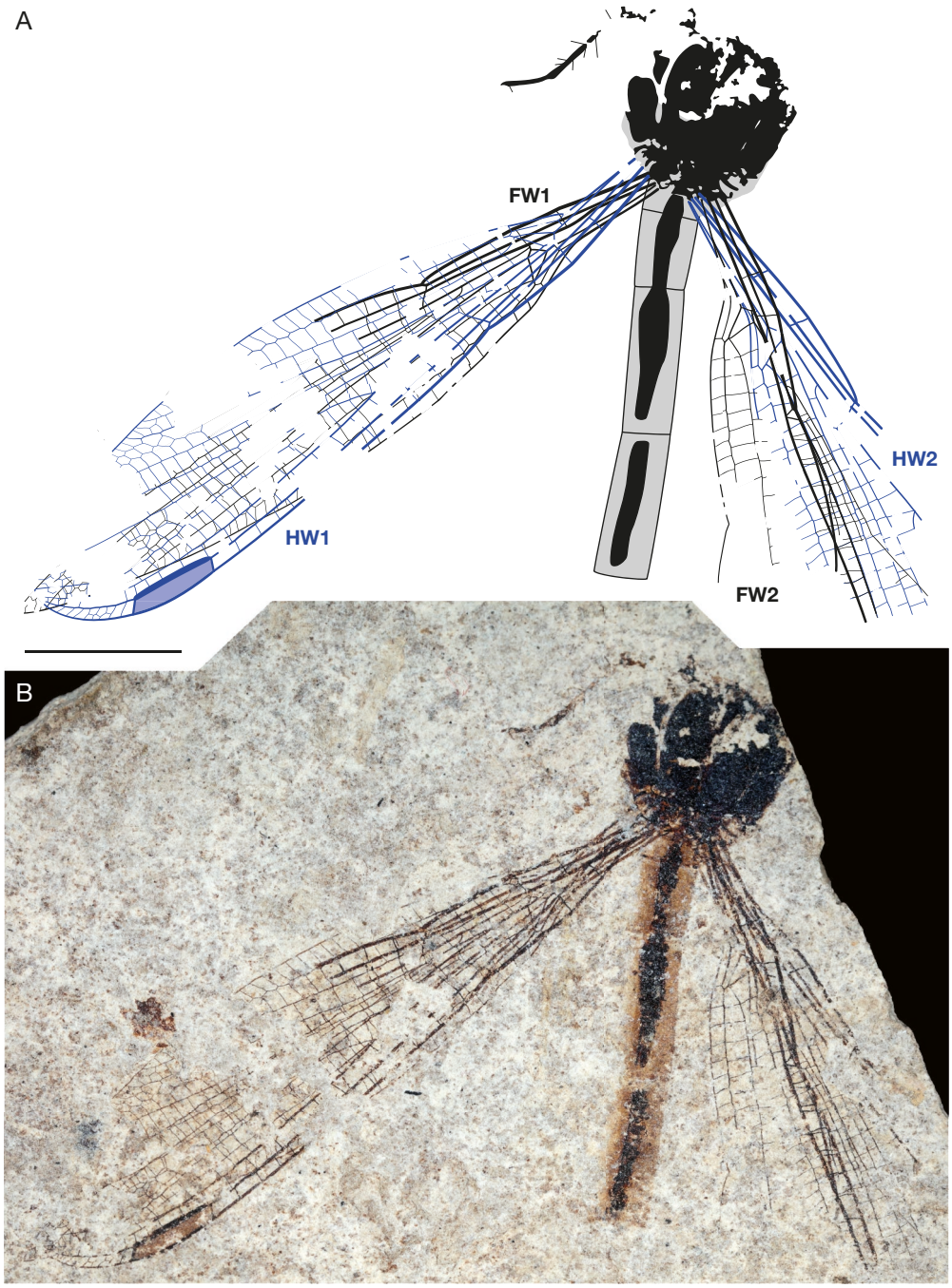

FIG. 1. — *Palaeophylolestes distinctus* n. gen., n. sp., holotype specimen (BDL 2002), overview; **A**, drawing; **B**, photograph (embedding matrix used as white reference). Scale bar: 5 mm.

DESCRIPTION

General aspects

Specimen preserving thoracic segments, fragments of a leg, 4 abdominal segments, and more or less complete wings, with pairs of one side largely overlapping; forewing of second pair (FW2) very damaged, creased along multiple folds, with a main disruption running along MA-MP area.

Wing venation (essentially derived from HW1)

Two antenodals in ScP-R area ; at least 8 postnodals (as preserved in HW1), probably 11 or 12 originally in hindwing, and probably more in forewing; subnodus short, oblique ; crossveins between RA and RP1/RP1+2 aligned with postnodals near nodus, slightly misaligned with them near pterostigma; pterostigma extending over four cells (in the RA-RP1 area); quadrangle trapezoidal (as opposed to quadrangular) with proximal edge about ½ of posterior edge in forewing, less than ½ in hindwing (i.e. quadrangle slightly narrower and longer in hindwing); RP1+2 / RP3+4 fork located closer to nodus than to arculus; Irp_{1+2}-rp_{3+4} starts opposite subnodus ; RP1 / RP2 fork located proximally, just before postnodal 4; area between Irp_1-rp_2 and RP2 with 3 rows of cells at

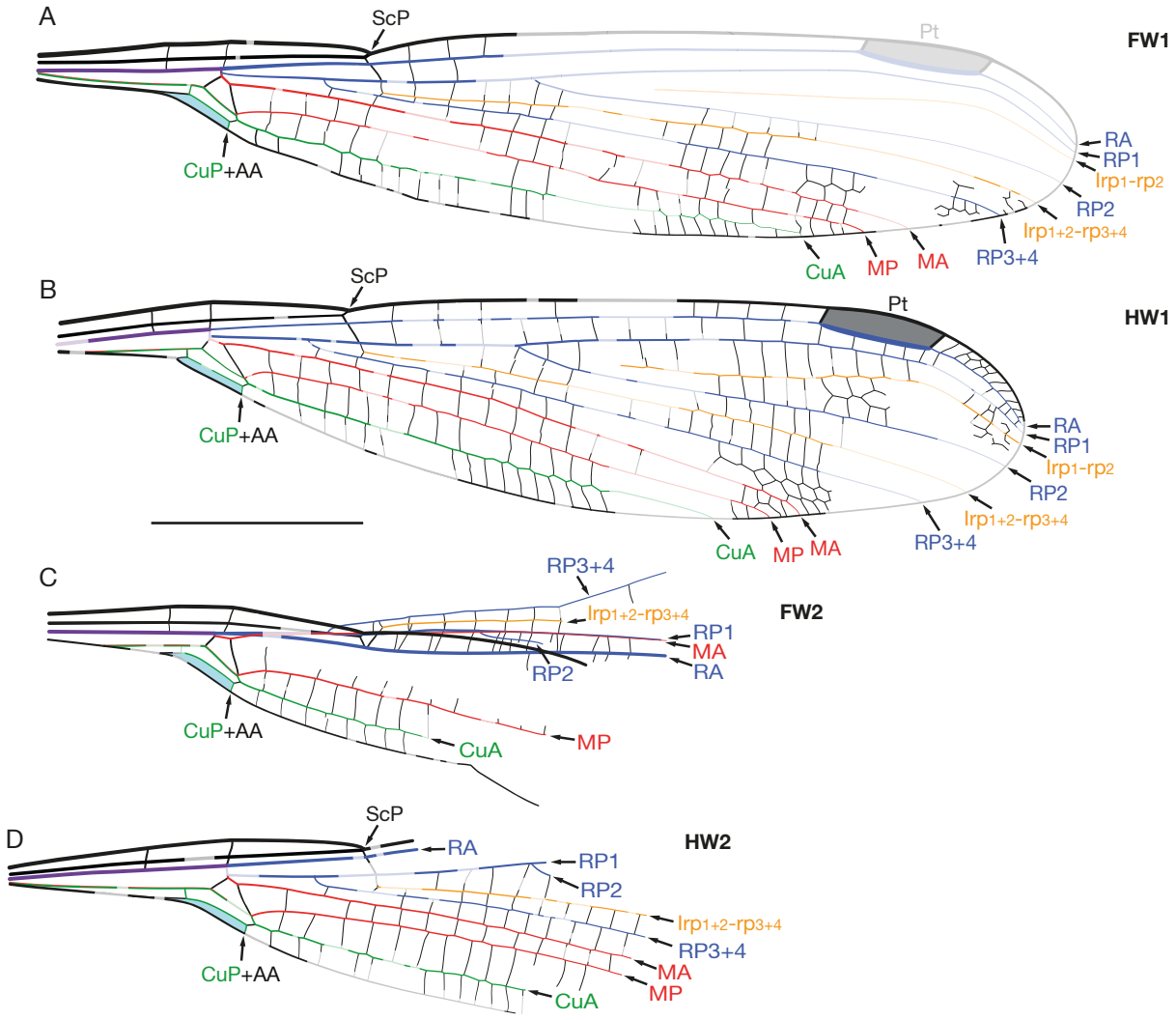

Fig. 2. — *Palaeophylolestes distinctus* n. gen., n. sp., holotype specimen (BDL 2002), drawings of wings, isolated (see Fig. 1 for their respective locations; faded vein portions reconstructed); **A**, **B**, first pair (located on the left side of the complete specimen); **A**, forewing; **B**, hindwing; **C**, **D**, second pair (located on the right side of the complete specimen); **C**, forewing; **D**, hindwing. Scale bar: 5 mm.

its broadest (probably forming one or two supplementary sectors); RP3+4-MA area broadening near posterior wing margin (broader than surrounding areas), with at least 3 rows of cells; MA very long, reaching posterior wing margin opposite beginning of pterostigma in hindwing (as observed in HW1), possibly longer in forewing (opposite pterostigma mid-length); MA-MP area with a single row of cells except in most distal part (preserved in hindwing, possibly present in forewing); MP slightly arched upwards at its point of divergence from MP+CuA, simple and rectilinear, long; MP-CuA area comparatively broad (broader than the MA-MP area), with a single row of cells; CuA long, mostly parallel to posterior wing margin; a single row of cells between CuA and posterior wing margin; cell located below sub-discoidal (i.e. sub-quadrangular) cell (i.e. anteriorly delimited by AA) well-developed, longer than sub-discoidal cell; in most areas cross-venation scalariform and forming quadrangular cells; cross-veins sigmoidal, reticulated and denser distal to pterostigma, reticulated near apex, and in RP3+4-MA area.

Dimensions

Forewing, length about 25.4 mm, maximum width about 4.9 mm (both estimated from FW1); hindwing, length 23.6 mm, width 5.3 mm (deduced from HW1).

Remarks

Within Lestoidea (as delimited in Bybee *et al.* 2021; and see Kohli *et al.* 2021), the new specimen can be assigned to the Synlestidae based on a particular combination of character states. The occurrence of the state 'RP1+2 / RP3+4 fork located closer to nodus than to arculus' is unique to this family indeed (see Garrison *et al.* [2010] and Fig. 3; the RP1+2 / RP3+4 fork is located closer to the arculus in Lestidae, Menatlestidae and Eolestidae, very close or opposite to the nodus in Hemiphlebiidae, and beyond it in Perilestidae; exceptions occur within Synlestidae, see Fig. 3B; see Bridges 1994, Greenwalt & Bechly 2014, Nel & Jouault 2022). This assignment is also consistent with the position of the arculus being closer to the nodus than to the wing

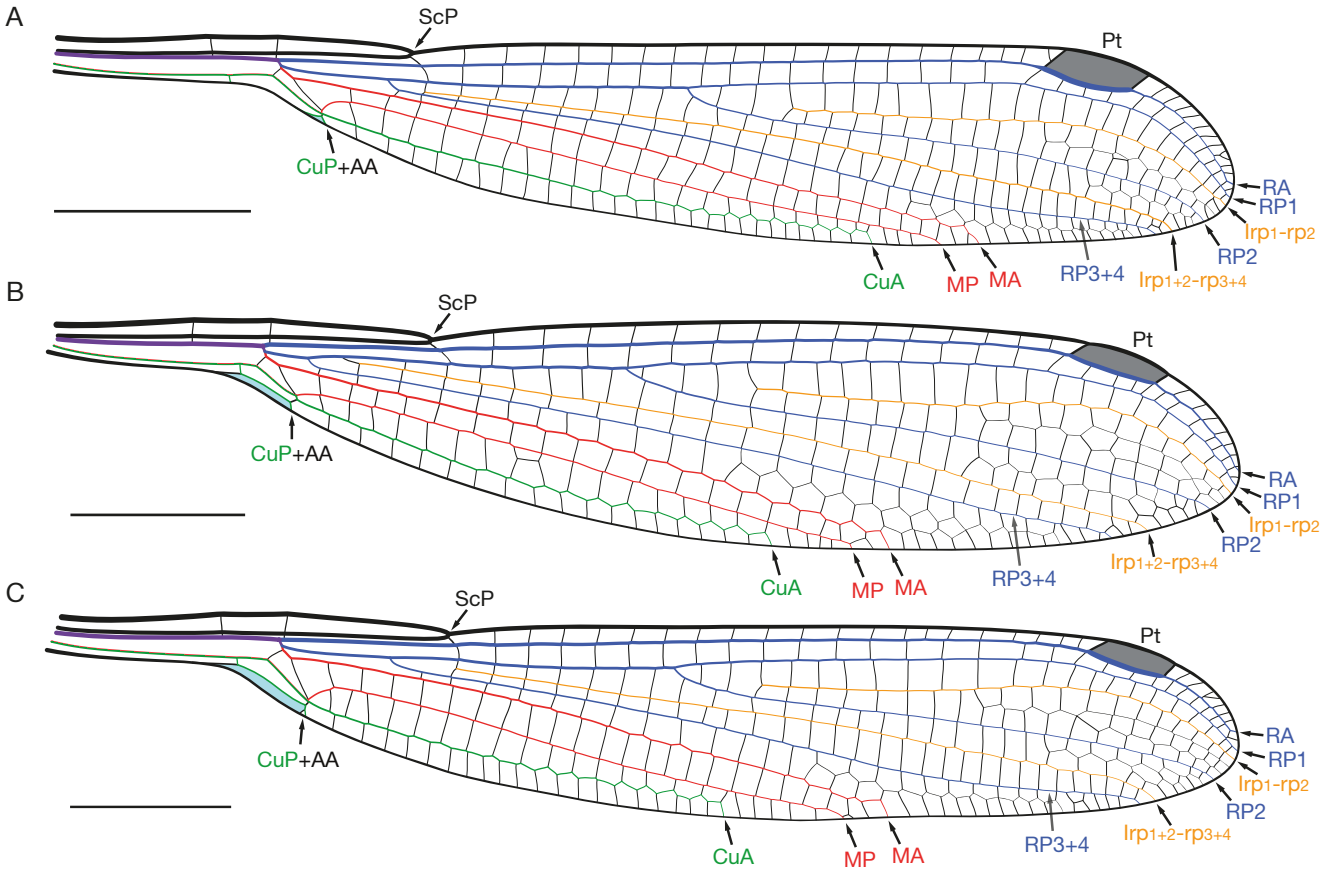

FIG. 3. — Forewings of selected extant representatives of the Synlestidae Tillyard, 1917: **A**, *Synlestes weyersii* Selys Longchamps, 1868 (male; based on photograph by John Tann [Sydney, Australia], CC BY 2.0); **B**, *Megalestes gyalsey* Gyeltshen, Kalkman & Orr, 2017 (male; based on Payra *et al.* 2021: fig. 2F, approximate scale); **C**, *Phylolestes ethelae* Christiansen, 1947 (male; based on Garrison *et al.* 2010: fig. 527). Scale bars: 5 mm.

base (see Tillyard 1917; more or less midway between the base and the nodus in Lestidae; closer to the wing base in Hemiphlebiidae, Eolestidae and Menatlestidae; conversely, very close to the nodus in Perilestidae), and the presence of intercalary veins in the area between Irp_1-rp_2 and RP2 (absent in Hemiphlebiidae and Perilestidae; also present in Lestidae, Eolestidae and Menatlestidae).

It must be mentioned that, outside of Lestoidea, the Megapodagrionidae and the Coenagrionidae also display the state 'RP1+2 / RP3+4 fork located closer to nodus than to arculus'. However, assignment to the former can be excluded owing to the quadrangular shape of the quadrangle. As for the latter, Coenagrionidae have a single row of cells in the area between Irp_1-rp_2 and RP2, while the new material has 3, as in Synlestidae.

The new specimen differs from all known Synlestidae by the very long MA, MP and CuA. Also, the quadrangle, characterised by a comparatively long proximal edge, is atypical compared to known Synlestidae. Additionally, unlike in *Synlestes* Selys Longchamps, 1868 (see Fig. 3A) and a number of other extant genera, including *Chlorolestes* Selys Longchamps, 1862b, *Ecchlorolestes* Barnard, 1937, *Episynlestes* Kennedy, 1920 and *Sinolestes* Needham, 1930 (see Bridges 1994; Simaika *et al.* 2020; and references therein) as well as some extinct genera such as *Madres* Petrulevičius, 2018 and *Inacayalestes* Petrulevičius, 2015 (both Eocene, Argentina), the cell located below the sub-discoidal cell (colour-coded in light blue in Figs 2, 3) is well-developed (i.e. AA diverges from the posterior margin in a basal position) in the new specimen. This state is shared with species of *Megalestes* Selys Longchamps, 1862a (Fig. 3B) and the monotypic genus *Phylolestes* Christiansen, 1947 (Fig. 3C). It is likely a plesiomorphic condition. The new specimen sharply differs from *Megalestes* spp. in the location of the RP1+2 / RP3+4 fork (unusually basal, for a Synlestidae, in *Megalestes*). Finally, the new specimen is overly similar to *Phylolestes ethelae* Christiansen, 1947. However, in addition to traits highlighted above, RP3+4 is more rectilinear in the new specimen (distally, it remains parallel to the posterior wing margin for some distance in *Phylolestes ethelae*). Finally, comparison with *Cretaphylolestes cretacicus* Huang, Fu, Lian, Gao & Nel, 2022 (Lower Cretaceous, China) is made difficult by the fragmentary state of the available material. Moreover, the overlapping of elements belonging to fore- and hindwing jeopardizes the identification of critical elements, such as the quadrangle shape, in this species. Given the above, the erection of a new species and genus is justified.

CONCLUSION

Given the extant distribution of the Synlestidae (see above), the discovery of a new representative in the western Palaearctic area is, at first glance, unexpected. However, a Synlestidae was already been reported from the Eocene Baltic amber (Bechly & Wichard 2008). Moreover, climatic conditions at Menat ca. 60 million years ago, as deduced from the fossil flora, were globally warmer and more humid than they are nowadays (Tanrattana *et al.* 2020). Considering that such conditions are favourable to the diversity of extant Odonata (Kalkman *et al.* 2008), as well as the extensive dispersal capacities of these insects (Corbet 2004; Sánchez-Herrera & Ware 2012), this new occurrence could have been anticipated indeed.

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