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Enigmaptera magnifica gen. nov, sp. nov., type genus and species of the new odonatopteran family Enigmapteridae, is described from the Moscovian of Avion (North of France). It is the sister group of the major clade Neodonatoptera, together in the new clade Paneodonatoptera. Its wing venation show important unique characters, never found in any other Odonatoptera. It is a further case of convergent wing petiolation in this superorder. *Enigmaptera magnifica*, like the protozygopteran *Jacquesoudardia magnifica* from the same outcrop, was probably living like the extant damselflies along the shores of lakes and rivers, hunting the small insects found in the same layers. These discoveries put a new light on the entomofaunistic diversity and complexity of the Late Carboniferous ecosystems.

Key words: Odonatoptera, fam., gen., sp. nov, phylogeny, Moscovian, palaeoecology.

THE CARBONIFEROUS represents the first period of well-documented diversification of major lineages of winged insects in the fossil record (Engel *et al.* 2013). It is well-known for the numerous very large to 'giant' insects (the popular meganeurids or griffenflies). But small to very small insects were also flourishing during this period. The recently discovered outcrop at Avion in the department of Pas-de-Calais, is especially rich in small to very small wings mixed with thousands of plant fragments. It has led a very diverse entomofauna that comprises Palaeodictyoptera (including larvae), Archaeorthoptera, Caloneurodea, Paoliida, Dictyoptera, and the oldest representatives of the clades Acercaria and Holometabola (Nel *et al.* 2013, Prokop *et al.* 2013, 2014, Coty *et al.* 2014). It is dated to the Moscovian (Westphalian C/D or equivalent Bolsovian/Asturian). The fossil insects were found in 'Terril N 7', which contains rocks from the slag heap of coal mines 3 and 4 of Liévin, Bolsovian (Westphalian C, 308–311 Ma, 'faisceaux de Ernestine') /Asturian (Westphalian D, 306–308 Ma, 'veines Arago, Dusouich, Marthe'; Bruno Vallois 2013 pers. comm.).

Here we describe a further very small wing that represents a new major clade of the superorder Odonatoptera. This wing is characterized by an extraordinary, unique pattern of wing venation. The Odonatoptera from Avion were already known by a Protozygoptera (*Jacquesoudardia magnifica* Prokop *et al.* 2014) and a Meganeuridae (*Gallotupus ourdardi* Nel *et al.* 2008).

Materials and methods

The material was collected by Patrick Roques. The fossil is provisionally stored in the collection of the Laboratory of Entomology in the Muséum National d'Histoire Naturelle, Paris (MNHN), France. The collection will ultimately be deposited in the Musée Géologique Pierre Vetter, Decazeville, France. The fossil was studied in a dry state using Olympus SZX-9 and Nikon SMZ 1500 stereomicroscopes. Line drawings of the venation pattern was drawn

directly with the aid of a camera lucida. Photographs were taken using a Canon D550 digital camera with MP-E 65mm and EF 50mm lenses. Original photographs were processed using the image-editing software Adobe Photoshop CS.

We mainly follow the wing venation nomenclature of Riek & Kukalová-Peck (1984), Nel *et al.* (1993), and Jacquelin *et al.* (2017). The venational symbols used here are specified as follows: symbols in capitals denote the longitudinal veins (Arc: 'arculus', Ax0: basal primary antenodal crossvein, ScA/ScP: subcostal anterior/posterior, RA/RP: radial anterior/posterior, IR: convex intercalary radial vein, MA/MP: medial anterior/posterior, CuA/CuP: cubital anterior/posterior, AA: anterior anal vein).

Systematic palaeontology

Class INSECTA Linnaeus 1758

Infraclass PALAEOPTERA Martynov 1923

Superorder ODONATOPTERA Martynov 1932

Clade **PANEODONATOPTERA** taxon nov.

Included taxon. The new family Enigmapteridae, and the Neodonatoptera Bechly, 1996.

Etymology. Named in reference to the clade Eodonatoptera.

Autapomorphies. Wings slender and elongate; MP and Cu are at least shortly fused. The autapomorphies of the Neodonatoptera becoming: R and MA basally appressed together.

Family ENIGMAPTERIDAE fam. nov.

Type species. *Enigmaptera magnifica* gen. nov, sp. nov.

Diagnosis. Wing characters only: very narrow wing, basal part of MA closely parallel to R complete distal fusion of MP with R and MA, strongly convex MA re-emerging from R in

arculus; very narrow anal area, CuP and CuA reduced to 'crossveins' between MP+Cu and AA, RP1/2 very long.

Enigmaptera gen. nov.

Type species. *Enigmaptera magnifica* sp. nov.

Diagnosis. Very small wing, only 2.9 mm wide, and ca. 14 mm long.

Etymology. Named after the surprising and enigmatic wing venation of this taxon.

Enigmaptera magnifica sp. nov.

(Figs. 1-2)

Holotype. Specimen Avion 35 (counterimprint of basal half of a wing), collected by Patrick Roques; provisionally stored in the collection of the Entomological Laboratory, MNHN, Paris, France. The collection will be deposited in the Musée Géologique Pierre Vetter, Decazeville, France.

Locality and age. Moscovian (Westphalian C/D equivalent to Bolsovian/Asturian), 'Terril N 7', Avion, Pas-de-Calais, France.

Etymology. Named after the wonderful state of preservation of the preserved parts of this wing.

Diagnosis. As for the genus.

Description. Basal half of a wing, very well preserved, veins being with this normal convexity. Length of fragment 10.5 mm, width of wing 2.9 mm; C making a basal curve, no visible ScA nor Ax0; concave ScP straight, very long, progressively approximating C (width of area between C and ScP near wing base 0.45 mm, at distal part of fragment 0.1 mm), ScP ending on C at ca. 10.2 mm from wing base; six visible crossveins between C and ScP; convex R (distally RA) parallel to ScP, width of area between them 0.41 mm, with seven

preserved crossveins between them; convex RA and concave RP separating at 2.4 mm from wing base (arculus); RP separating into RP1/2 and RP3/4 just distally; base of convex secondary longitudinal vein IR2 just distal of point of separation of RP into RP1/2 and RP3/4; RP1/2, IR2, RP3/4 straight, with few crossveins between them defining long rectangular cells; fork of RP1/2, if present, in a very distal position, distal of apex of ScP; MA convex, but weaker and less convex than R, closely parallel to it, ending in R 2.3 mm from wing base, at the same point with MP; basal free part of concave MP oblique between base of MA and Cu, 0.8 mm long, ending into Cu; basal free part of Cu 0.7 mm long; concave CuP separating from Cu 0.2 mm basal of point of fusion between MP and Cu, and ending into AA, a Z-like kink in CuP at point of fusion with AA; CuA separating from MP 0.3 mm distal of point of fusion of CuA with MP, a Z-like kink in CuA at point of fusion with AA; MP anteriorly curved and ending into R at the same point with MA; MA re-emerging from R at the same point with RP (arculus), very convex, 0.9 mm long before its fusion with CuA+CuP+AA; then MA very straight; convex AA straight, progressively diverging from posterior wing margin and ending into MA; area between AA and posterior wing margin very narrow, 0.4 mm at its maximum width, 0.05 mm wide near wing base.

Discussion. This small wing is remarkable in the presence of a point of fusion of R, MA and MP 2.3 mm from wing base, with an arculus just distal to this point. *Enigmaptera* gen. nov. can be attributed to the Odonatoptera Martynov, 1932 because it has the following synapomorphies: wings with relatively undeveloped anal area; MP unbranched; anal brace with a Z-like kink in CuP and in CuA at their points of fusion with AA; ScP fuses with the costal margin distinctly basal of wing apex (Bechly 1996). *Enigmaptera* shares with the Palaeodonatoptera Petrulevičius and Gutiérrez, 2016 the apomorphic fusion of MP with Cu, while the Eugeroptera Petrulevičius & Gutiérrez 2016 (only Eugeropteridae Riek 1983) have a vein M separated from Cu (at least in hind wing, probably in forewing too). Petrulevičius

and Gutiérrez (2016) divided the clade Palaeodonatoptera into the Kukaloptera Petrulevičius & Gutiérrez 2016 and Plesiodonatoptera Petrulevičius & Gutiérrez 2016 [= (Argentinalidae Petrulevičius & Gutiérrez 2016 (Geropteridae Petrulevičius & Gutiérrez 2016 & Neodonatoptera Bechly 1996))]. *Enigmaptera* shares with the Neodonatoptera the synapomorphy 'MP fused with Cu for a long distance', while in the Kukaloptera, Argentinalidae, and Geropteridae, MP is only fused for a short distance with CuA.

Nevertheless, in *Enigmaptera*, MA is distinctly separated from MP at wing base but still not fused with R, a very particular situation present in Eugeroptera, the Kukaloptera, the Argentinalidae, and the Geropteridae (Petrulevičius & Gutiérrez 2016, Jacquelin *et al.* 2017), but not in the Neodonatoptera in which MA is appressed or fused to R, even in the most 'basal' clade Eomeganisoptera Rohdendorf 1962 (viz. Erasipteridae Carpenter 1939). Thus *Enigmaptera* corresponds to a completely new clade, sister group of the Neodonatoptera

Enigmaptera is characterized by several autapomorphies: complete distal fusion of MP with R and MA, the strongly convex MA re-emerging from R in the arculus; very narrow wing, very narrow anal area, and very long RP1/2.

Palaeoecological inferences

The sub-petiolation of *Enigmaptera* is remarkable. Few Carboniferous petiolate wings of Odonatoptera are known, viz. the Protozygoptera *Bechlyia* Jarzembowski & Nel 2002 (Farrington Formation, Upper Westphalian D, Kasimovian, UK) and *Jacquesoudardia* (Avion), the meganisopteran Bechalidae (*Bechala* Ilger & Brauckmann 2012, Namurian, Germany) and the Meganeuridae *Gallotupus ourdardi* (which has a short petiole, also from Avion) (Jarzembowski & Nel 2002, Nel *et al.* 2008, 2012; Prokop *et al.* 2014). *Enigmaptera* is a further convergent case of 'long' petioles (longer than the width) occurring in Odonatoptera. The others concern the Protozygoptera (Late Carboniferous to Early

Cretaceous), the Triadophlebiomorpha (Triassic), Zygoptera (Mesozoic to recent), Stenophlebioptera (Mesozoic), and Epiophlebioptera (Cretaceous to recent). All these previously known cases concerned taxa belonging to the derived clade Discoidalia Bechly 1996 (characterized by the presence of a nodus and of a discoidal cell). *Enigmaptera* has no nodal structure, but a kind of 'basal complex' sensu Rajabi *et al.* (2016), viz. a structure composed by the shared point of fusion of MA, MP and R together with bases of RP and distal part of MA; plus the cell defined by CuA, MP ending into R, and distal part of MA (Fig. 2). It is analogous, but not homologous, to the arculus plus discoidal cell of a Discoidalia and probably had the same function for deformations of the basal third of the wing.

Such small 'damselfly-like' Odonatoptera were probably living in close environments, hunting the small insects along the rivers or in forests, unlike the large to very large Meganisoptera, with wing span over 60 cm (Nel *et al.* 2009).

Data access statement

This study did not involve any underlying data. All specimens are available for re-study in the public institute indicated in the text.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Fig. 1. Enigmaptera magnifica gen. nov, sp. nov., holotype Avion 35, wing photograph and reconstruction (scale bars = 2 mm).

Fig. 2. Enigmaptera magnifica gen. nov, sp. nov., holotype Avion 35, wing base (scale bar 1 mm).

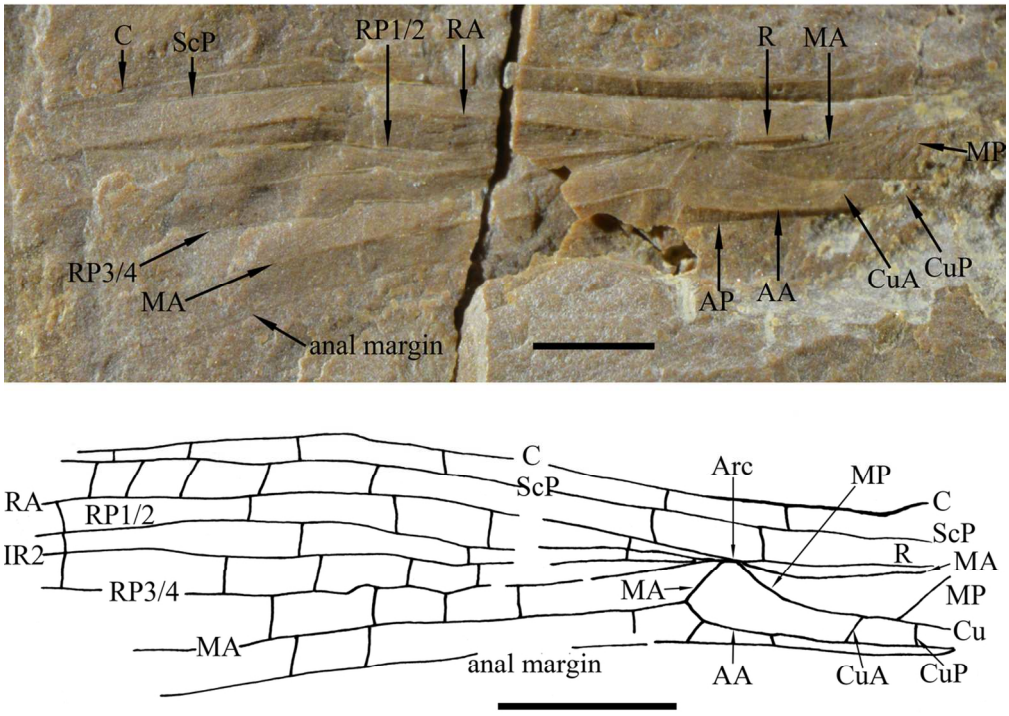

figure 1

113x86mm (300 x 300 DPI)

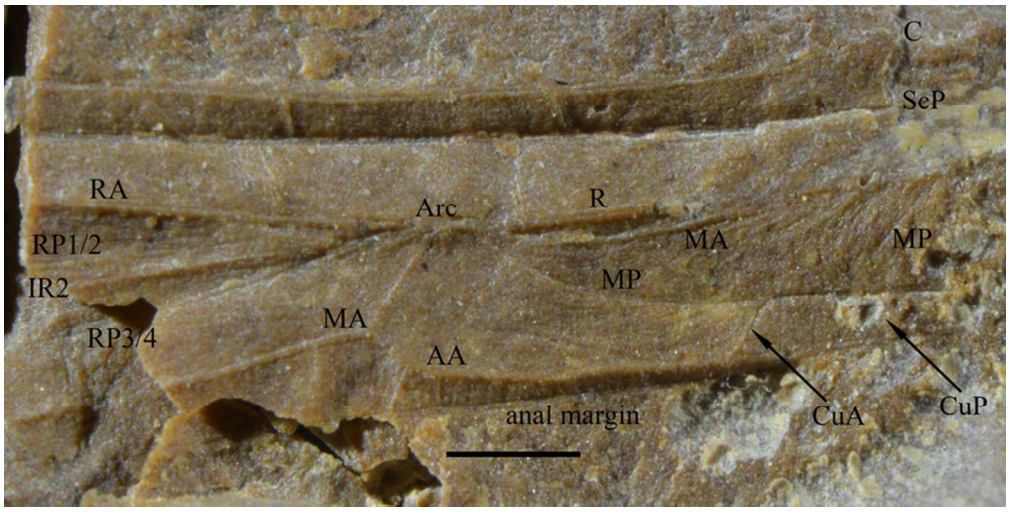

figure 2

75x37mm (300 x 300 DPI)