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4 A new strange Archaeorthoptera from the Moscovian of Avion (France) (Insecta, Polyneoptera)

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15

16 ABSTRACT

17 A new archaeorthopteran genus and species, *Avionugonioneura jouaulti*, is described from the  
18 Moscovian of the Avion in Northern France. It shows several strong similarities, with the two  
19 genera *Contracladus* (Pennsylvanian) and *Nugonioneura* (early Permian), **viz. a simple vein M**  
20 **emerging anteriorly from M+CuA+CuPa and an anteriorly branched CuA+CuPa**, which are  
21 putative synapomorphies, suggesting a possible attribution to the family Nugonioneuridae. This  
22 discovery confirms the very important diversity of the Archaeorthoptera in the outcrop of  
23 Avion.

24

25 KEYWORDS

26 Insecta; Polyneoptera; ?Nugonioneuridae; early late Carboniferous; diversity

27

## 28 **Introduction**

29 For a Moscovian outcrop, The Konservat-Lagerstätte of Avion (Northern France) is especially  
30 rich in polyneopteran insects of the superorder Archaeorthoptera (so-called ‘orthopteroid’  
31 insects), with no less than eight genera and nine species: *Aviogramma gracilis* Prokop et al.,  
32 2014 (plus another Caloneurodea), *Aviocladus pectinatus* Prokop et al., 2014, *Aviohapaloptera*  
33 *bethouxi* Prokop et al., 2014, *Aviologus duquesnei* Coty et al., 2014, *Cacurgus avionensis*  
34 Schubnel et al., 2020, *Beloatta duquesnei* Nel et al., 2021, cf. *Tococladus* sp. (Coty et al. 2014;  
35 Prokop et al. 2014; Schubnel et al. 2020; Nel et al. 2020).

36 Here we describe a further new genus and species belonging to a family different of  
37 those previously recorded, confirming the impressive diversity of the clade in this outcrop.

38

## 39 **Material and methods**

40 The fossil was found by one of us (P.R.) in the slag heap of Avion. It was examined under a  
41 Nikon SMZ1500 and photographed with an AmScope camera MU900.

42 We follow the wing venation terminology of Béthoux and Nel (2002).

43 Wing vein terminology: CuA, cubitus anterior; CuP, cubitus posterior; CuPa, anterior branch  
44 of CuP; CuPb, posterior branch of CuP; M, median vein; PCu, postcubital vein; RA, radius  
45 anterior; RP, radius posterior; ScP, subcosta posterior.

46

## 47 *Systematic palaeontology*

48 Superorder Archaeorthoptera Béthoux and Nel, 2002

49 Family ?Nugonioneuridae Carpenter, 1976

50 *Avionugonioneura* gen. nov.

51 Zoobank xxxx

52

53 *Type species*

54 *Avionugonioneura jouaulti* sp. nov.

55

56 *Diagnosis*

57 Forewing characters only. CuPa ending into M+CuA and not in a free CuA; no CuPa $\beta$ , vein  
58 M+CuA+CuPa anteriorly pectinate; ScP ending into costa; short posterior branches of  
59 CuA+CuPa; five simple branches of RP; M simple and strictly parallel to branches of RP and  
60 to first anterior branch of CuA+CuPa; area between RA and RP broad with two rows of cells.

61

62 *Etymology*

63 Named after the outcrop of Avion and the genus name *Avionugonioneura*. Gender feminine.

64

65 *Avionugonioneura jouaulti* sp. nov.

66 (Fig. 1)

67 Zoobank xxxx

68

69 *Etymology*

70 Named after our friend and colleague Corentin Jouault, for his contribution to  
71 Palaeoentomology.

72

73 *Type material*

74 MNHN.F.A71353 (two nearly complete forewings overlapped at rest), stored at the Muséum  
75 National d'Histoire Naturelle, Paris, France.

76

77 *Type locality*

78 ‘Terril N°7’, Avion, Pas-de-Calais, France.

79

80 *Stratigraphic occurrence*

81 Moscovian (Westphalian C/D equivalent to Bolsovian/Asturian).

82

83 *Diagnosis*

84 As for the genus by monotypy.

85

86 *Description*

87 Forewing elongate, 16.0 mm long, 5.0 mm wide; ScP reaching anterior wing margin at 8.7 mm  
88 from wing base; costal area rather narrow, 0.6 mm wide with no visible veinlet; a series of  
89 simple short crossveins in area between ScP and R; RP separating from RA 4.4 mm from wing  
90 base; area between RA and RP broad, 0.7 mm wide, with two rows of cells in its distal part,  
91 apically narrower; RA with a series of short, more or less curved anterior veinlets between it  
92 and anterior wing margin; apex of RA 2.4 mm of wing apex; RP with five posterior branches,  
93 three of them being forked again distally, parallel to M; RA and RP approximate in apical parts;  
94 a common stem R+M+CuA; M+CuA separating from R 2.5 mm from wing base, straight; M  
95 distally simple and straight, separating from CuA+CuPa 0.4 mm distal of point of fusion of  
96 CuPa with M+CuA; CuA+CuPa with at least an anterior simple branch parallel to M, and two  
97 weak posterior subapical branches; concave CuPa curved, elongate, 2.0 mm long, ending into  
98 M+CuA; concave CuPb straight and simple in its preserved part; convex PCu basally curved  
99 and simple in its preserved part; anal veins not preserved.

100

101 **Discussion**

102 This fossil is a pair of forewings in life position. It belongs to the Archaeorthoptera because of  
103 the following characters (Béthoux and Nel 2002): CuP differentiated into concave CuPa and  
104 CuPb; a common stem R+M+CuA, from which M+CuA separates distally; CuPa ending into  
105 M+CuA. *Avionugonioneura* gen. nov. does not fall into the Panorthoptera because CuPa is not  
106 differentiated into two branches CuPa $\alpha$  and CuPa $\beta$ ; MA1 and MA2 cannot be differentiated. It  
107 has a very peculiar vein M+CuA+CuPa, with two strong and simple anterior branches, which  
108 is rarely found among the Archaeorthoptera but also present in the Paoliida for CuA only  
109 (Prokop et al. 2014a). Similar pectinations are found in the Cnemidolestodea sensu Béthoux  
110 (2005), but with the important difference in the first branch being itself forked several times.  
111 Another difference to the members of Cnemidolestodea is the vein CuPa ending into M+CuA  
112 in *Avionugonioneura* gen. nov., while it ends into CuA in the Cnemidolestodea. Two  
113 Cnemidolestodea are already known from Avion, viz. *Aviocladus* Prokop et al., 2014 that  
114 differs from *Avionugonioneura* gen. nov. in ScP ending into R, and base of RP in a much distal  
115 position (Prokop et al. 2014b); and *Piesbergopterus avionensis* Nel and Roques, 2021 that  
116 differs from *Avionugonioneura* gen. nov. in the presence of a specialized area between an  
117 anterior branch of M and a posterior branch of the same vein (Nel and Roques, 2021). Few  
118 cases of Archaeorthoptera with CuPa ending into M+CuA and not in a free CuA are known. It  
119 is the case for *Bruaylogus magnificus* Coty et al., 2014, but this taxon has a CuPa $\beta$  as  
120 panorthopteran synapomorphy, and no anterior pectination of CuA+CuPa (Coty et al. 2014; Gu  
121 et al. 2017). *Nugonioneura* Tillyard, 1937 (*N. problematica* Tillyard, 1937 known from the  
122 Lower Permian of Elmo in Kansas, U.S.A.) (Tillyard 1937; Aristov 2020, p. 6, Figs 3, 4) and  
123 *Contracladus impar* Dvořák et al., 2021 (Pennsylvanian of Piesberg, Germany) also have no  
124 CuPa $\beta$ , a simple M anteriorly emerging from vein M+CuA+CuPa, and an anterior branch of  
125 CuA+CuPa parallel to M, as in *Avionugonioneura* gen. nov. Both differ from

126 *Avionugonioneura* gen. nov. in ScP ending into RA, the presence of an angle in M below base  
127 of RP so that these two veins approximate, no posterior branch of CuA+CuPa, shorter anterior  
128 branches of CuA+CuPa. *Nugonioneura* has only three simple branches of RP instead of five  
129 with some being forked again more distally in *Avionugonioneura* gen. nov. and *Contracladus*.  
130 M is distally forked in *Contracladus*, instead of being simple as in *Avionugonioneura* gen. nov.  
131 and *Nugonioneura*.

132 As a conclusion, *Contracladus*, *Nugonioneura*, and *Avionugonioneura* gen. nov. can  
133 only be considered as Archaeorthoptera of uncertain affinities. A new phylogenetic analysis  
134 will be necessary to clarify their positions, even if they possibly all belong to the same  
135 archaeorthopteran family Nugonioneuridae that would be characterized by the putative  
136 apomorphies: ‘CuPa ending into M+CuA’, a ‘simple M anteriorly emerging from  
137 M+CuA+CuPa’, and ‘presence of a simple anterior branch of CuA+CuPa’.

138

139 Remarks. Coty et al. (2014: 464, fig. 1) described and figured a wing fragment they attributed  
140 to a ‘cf. *Tococladus* sp.’ (Cnemidolestodea Tococladidae). It strongly resemble the wing apex  
141 of *Avionugonioneura* gen. nov. in the number of branches of RP, simple M and anterior  
142 branches of CuA+CuPa, and RA and RP strongly approximating distally. The only difference  
143 is the area between RA and RP narrower in the putative ‘cf. *Tococladus* sp.’ than in  
144 *Avionugonioneura* gen. nov. Numerous Palaeozoic wings of Polyneoptera have very similar  
145 patterns of venations in their distal parts. They can be discriminated and attributed to precise  
146 clades only on the basis of the basal halves of the wings.

147 Rasnitsyn and Aristov (2021: 151) indicated that in *Tococladus garrici* Béthoux et al., 2003,  
148 the vein ‘CuPa’ is convex, after the original photograph in Béthoux et al. (2003: fig. 4),  
149 suggesting that the attribution of the Tococladidae to the Archaeorthoptera could be not well-  
150 grounded. But the original photograph shows a CuPa of ‘intermediate’ convexity compared to

151 those of the convex M+CuA and the concave stem of CuP. Also Béthoux et al. (2003) did not  
152 indicate anything about the convexity of this vein. This uncertainty in the determination of  
153 the convexity of the vein CuPa is due to fossilization, but it is clear that this vein has a diameter  
154 and shape different of the more distal vein CuA+CuPa, supporting that it is a branch of CuP  
155 and not CuA. Thus the argument of Rasnitsyn and Aristov (2021) does not stand.

156

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160

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210

211 Figure 1. *Avionugonioneura jouaulti* gen. et sp. nov., holotype MNHN.F.A71353. (A)  
212 photograph of habitus; (B) forewing reconstruction, arrowhead: M+CuA, arrow: CuPa. Scale  
213 bars = 1 mm.

214

