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► **To cite this version:**

André Nel, Bruno Vallois, Hervé Duquesne. A new archaeorthopteran family from the late Carboniferous of La Mure (France). *Historical Biology*, 2022, 35 (2), pp.264-267. 10.1080/08912963.2022.2034804 . hal-03566590

HAL Id: hal-03566590

<https://hal.sorbonne-universite.fr/hal-03566590>

Submitted on 11 Feb 2022

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1 Historical Biology

2

3 A new archaeorthopteran family from the late Carboniferous of La Mure (France)

4

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6

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14

15 ABSTRACT

16 The new archaeorthopteran family Roqueiidae is defined for the new genus and species *Roqueia*
17 *alpine*, described from the Pennsylvanian (Kasimovian) of La Mure region (Isère, Alps,
18 France). This new taxon is characterized by the set of characters: basal fusion of MA with R,
19 its distal re-emergence from RP, and ending into vein MP. The Roqueiidae are tentatively
20 assigned to the order Cnemidolestodea together with the family Cnemidolestidae.

21

22 KEYWORDS

23 Insecta; ?Cnemidolestodea; fam., gen. et sp. nov.; Kasimovian, French Alps.

24

25 **Introduction**

26 The superorder Archaeorthoptera Béthoux and Nel, 2002 (total group of the extinct and extant
27 Orthoptera) reached a maximum of diversity during the late Paleozoic, with no less than four
28 major orders (Cnemidolestodea, Caloneurodea, Titanoptera, crown Orthoptera) plus a series of
29 families and genera representative of the stem group of the Panorthoptera. This diversity greatly
30 decreased during the Triassic with only the Titanoptera and crown Orthoptera surviving and
31 again after the extinction of the Titanoptera near the end of this period. An impressive series of
32 recent discoveries of new Archaeorthoptera is going on, always confirming this general
33 tendency of a highest diversity of the group during the late Carboniferous and the Permian (e.g.,
34 Schubnel et al. 2021).

35 Here we describe a new fossil Archaeorthoptera with a unique forewing venation from the
36 Kasimovian of the French Alps. It is probably related to the order Cnemidolestodea sensu
37 Béthoux (2005), but corresponds to a new family, genus, and species.

38

39 **Material and methods**

40 The fossil was found by one of us (H.D.) in the slag heap of the Villaret. It was examined under
41 a Nikon SMZ1500 and photographed with an AmScope camera MU900. This outcrop
42 corresponds to the Kasimovian (Baruellian, Stephanian A), with *Crenulopteris lamuriana*
43 (Heer) as typical plant of the biozone (Wittry et al., 2014). We follow the wing venation
44 terminology of Béthoux and Nel (2002), modified by Schubnel et al. (2020).

45 Wing vein terminology: A, anal vein; C, costa; CuA, cubitus anterior; CuP, cubitus posterior;
46 CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; MA, median anterior vein; MP,
47 median posterior vein; PCu, postcubital vein; RA, radius anterior; RP, radius posterior; ScP,
48 subcosta posterior.

49 urn:lsid:zoobank.org:pub:2D28E9D1-82FC-4351-B7AF-AD6C3950F08F

50

51 *Systematic Palaeontology*

52 Superorder Archaeorthoptera Béthoux and Nel, 2002

53 ?Order Cnemidolestodea Handlirsch, 1937 (sensu Béthoux 2005)

54 Family Roqueiidae fam. nov.

55 urn:lsid:zoobank.org:act:C87D6416-9EB8-40CD-8A51-8BADF019AFB1

56 *Type genus*

57 *Roqueia* gen. nov.

58

59 *Diagnosis*

60 Wing characters only. In forewing, fusion of MA with R and distal re-emergence independently
61 of MP+CuA (putative apomorphy, convergently present in the Cacurgidae); MA re-emerging
62 from RP and ending into MP (putative autapomorphy); separation of MP from CuA basal of its
63 fusion with CuPa; short stem of MP before its first posterior branch; ScP ending into C.

64 .

65

66 Genus *Roqueia* gen. nov.

67 urn:lsid:zoobank.org:act:2A691E2A-8496-468F-BE84-193D42BEB7A8

68

69 *Type species*

70 *Roqueia alpina* sp. nov.

71

72 *Etymology*

73 Named after Patrick Roques, for his very efficient and kind help in the research on
74 Carboniferous insects. Gender Feminine.

75

76 *Diagnosis*

77 As for the family, plus the following forewing characters: two posterior branches of MP basal
78 of its distal fusion with MA; two posterior branches of MA+MP basal to its fusion with RP

79

80 *Roqueia alpina* sp. nov.

81 (Figs 1, 2)

82 urn:lsid:zoobank.org:act:546938FF-8C99-401B-A8AD-3AD8E98A37BC

83

84 *Etymology*

85 Named after the Alp mountains.

86

87 *Holotype*

88 Specimens Fa 0145 (imprint) and Fa 0145b (counterimprint) (fragments of legs, a nearly
89 complete forewing, a less well-preserved forewing and a hind wing), stored at the Musée
90 d'Histoire Naturelle of Grenoble, France.

91

92 Type locality

93 Slag heap of the Villaret, Susville, La Mure, Matheysine region, Isère, France

94

95 *Stratigraphic occurrence*

96 Kasimovian (Stephanian A), 'étage productif du houiller' of La Mure.

97

98 *Diagnosis*

99 As for the genus by monotypy.

100

101 *Description*

102 Forewing 35.4 mm long, 12.0 mm wide; area between C and ScP 1.5 mm wide; ScP straight,
103 apically weakening and ending in C 23.8 mm from wing base; area between ScP and R as broad
104 as that between C and ScP, with poorly preserved crossveins in basal part and elongate anterior
105 branches of RA in distal part; area between C and RA broad with a series of complex branched
106 veinlets in-between; base of RP 13.1 mm from wing base; RA weakly curved posteriorly; RP
107 emitting a very strong posterior branch very close to its base, this branch ending into MP,
108 interpreted as MA captured by R, fused with RP, and re-emerging distally to end into MP; main
109 branch of RP long before its distal fusion with MA+MP; RP with three to four posterior
110 branches; an elongate broadly triangular area limited by RP, MA and MP, apparently free of
111 crossveins; MP+CuA basally fused with R, separating from it ca. 4.5 mm from wing base; stem
112 of MP+CuA 4.1 mm long; MP weakly sigmoidal, very long before its fusion with MA, defining
113 an elongate triangular area with R, RP+MA, and MA, this area with four faint crossveins; MP
114 with two posterior branches basal to its fusion with MA; MA+MP with two posterior branches
115 basal to its fusion with RP; basal free part of CuA very short, 1.4 mm long; an elongate CuPa
116 ending into CuA; CuA+CuPa nearly straight, with two posterior branches; a broad area between
117 CuA+CuPa, CuPa and CuPb; CuPb simple and nearly straight; PCu strongly arched and
118 touching CuP in one point; two anal veins visible.

119 Hind wing poorly preserved, lying over second forewing, ca. 33.7 mm long, ca. 11.9 mm wide,
120 without visible anal fan; no triangular elongate area between R and first anterior branch of
121 MP+CuA+CuPa present.

122 Leg fragments poorly preserved, but tibia and femur elongate and relatively thin (Fig. 2B).

123

124 **Discussion**

125 This fossil is attributed to the Archaeorthoptera as it shares the main diagnostic characters of
126 this superorder, namely the basal fusion of CuA with M (only its distal part MP+CuA being
127 preserved) and subsequent connection of CuA with an anterior branch CuPa of CuP (Béthoux
128 and Nel 2002: fig. 1). The elongate CuPa and the absence of an elongate vein between CuPa
129 and CuPb exclude any affinities with the Panorthoptera. *Roqueia* gen. nov. has some similarities
130 with the Oedischiidae that have also a triangular area between RP and M. But the presence of
131 four posterior branches of MP also excludes affinities with this orthopteran group in which
132 there is a single vein MP separating from the anterior branch MA that is itself parallel to R/RP
133 and ending into RP. Also the Oedischiidae have an anal fan in the hind wing, unlike *Roqueia*
134 gen. nov.

135 *Roqueia* gen. nov. shows important similarities with the archaeorthopteran genera
136 *Omalietta* Béthoux and Nel, 2005 (*O. ramosa* Béthoux and Nel, 2005 and *O. polonica* Dvořák
137 et al., 2019) and *Omalia* Van Beneden & Coemans, 1867 in the following characters: ScP not
138 ending into RA, CuPa fused with CuA distal of the base of M, M shortly touching RP. But
139 *Omalietta* and *Omalia* have branches MP and MA distally separating from a long stem M and
140 no strong oblique vein in area between M and RP (Béthoux and Nel, 2005; Dvořák et al., 2019).

141 Furthermore, *Roqueia* gen. nov. has some characters very similar to those of the order
142 Cnemidolestodea (sensu Béthoux, 2005, to include the Cnemidolestidae only), such as a
143 specialized elongate triangular area between RP/MA and a long vein emerging from M+CuA,
144 distally closed by the fusion of these veins; plus the vein MP emitting several parallel posterior
145 branches. Notice that Aristov (2014) proposed a different definition of the Cnemidolestodea to
146 include much more families in this order, but there is no clear synapomorphy supporting this
147 order sensu Aristov (see Dvořák et al. 2021; Nel and Poschmann 2021).

148 *Roqueia* gen. nov. strongly differs from the Cnemidolestidae in the absence of a free
149 MA separating from MP+CuA. The specialized triangular area in *Roqueia* gen. nov. is between

150 RA and MP, not between MA and the first anterior branch of MP+CuA+CuP; and MP is
151 separating from CuA basal to fusion of CuA with CuPa. In this area of *Roqueia* gen. nov., there
152 is a very strong oblique vein emerging from RP and ending into MP, which can only correspond
153 to MA basally fused with R and re-emerging distally from RP, a character also present in few
154 other Archaeorthoptera (e.g., Cacurgidae, see below). In the Cnemidolestidae, the vein MA is
155 basally separating from MP+CuA and closely parallel to R/RP (Langiaux and Parriat 1974;
156 Whalley 1979; Pinto and Pinto de Ornellas 1980; Béthoux and Nel 2005; Béthoux 2005;
157 Martins-Neto et al. 2007; Gu et al. 2011, 2014; Aristov 2013, 2014; Dvořák et al. 2021; Nel
158 and Poschmann 2021). The narrow area between MA and R/RP of the Cnemidolestidae is no
159 longer present in *Roqueia* gen. nov. *Roqueia* gen. nov. could have some similarities with *Ivkinus*
160 Aristov, 2014 (currently in the family Sylvabestiidae Aristov, 2000) in the presence of a
161 triangular area between R/RP and M with several oblique crossveins in-between, but this last
162 taxon is based on a rather poorly preserved fossil in which the vein CuPa is not preserved. Also
163 Aristov (2014: fig. 13) considered that the vein M of *Ivkinus* is basally separated from CuA and
164 distally forked into MA (ending into RP) and a free MP, which is a pattern completely different
165 from that of *Roqueia* gen. nov.

166 A further, less important difference of *Roqueia* gen. nov. is the ScP ending in C, instead
167 of RA in the genera of Cnemidolestidae (this character is subject to several homoplasies in the
168 Archaeorthoptera).

169 The hind wings of the Cnemidolestidae are generally less well-known than their
170 forewings. They are also less ‘complex’, without a well-defined triangular elongate area
171 between MA and first anterior branch of MP+CuA+CuPa (Béthoux and Nel 2005). Their anal
172 area are generally unknown, even in the well-preserved genus *Protodiamphipnoa* Brongniart,
173 1885.

174 The genera of the panorthopteran family Cacurgidae Handlirsch, 1911 share with
175 *Roqueia* gen. nov. the two characters ‘fusion of MA with R and its distal re-emergence
176 independently of MP+CuA’ and ‘separation of MP from CuA basal of its fusion with CuPa’
177 (Schubnel et al. 2019). They also share the characters ‘ScP ending into C’, ‘presence of a
178 posterior branch of MP basal of its distal fusion with MA’, and ‘presence of posterior branches
179 of MA+MP basal to its fusion with RP’. The main differences between *Cacurgus* Handlirsch,
180 1911 and *Roqueia* gen. nov. are the presence of a first posterior branch CuPa β of CuPa
181 (characteristic of the Panorthoptera), and the re-emergence of MA directly from R in the former,
182 while it re-emerges from RP in the latter. *Cacurgus* also differs from *Roqueia* gen. nov. in the
183 very long stem of MP before its first posterior branch.

184 The character ‘MA captured by R and distally re-emerging independently of MP+CuA’
185 occurred at least two times in the superorder Archaeorthoptera. The very distal re-emergence
186 of MA from RP instead of stem of R is a putative autapomorphy of *Roqueia* gen. nov. The
187 general pattern of the presence of an elongate triangular area anteriorly and distally limited by
188 R and RP and posteriorly by MP could be a putative synapomorphy of *Roqueia* gen. nov. with
189 the Cnemidolestidae. Nevertheless, this hypothesis would need to be tested by a phylogenetic
190 analysis of the whole Archaeorthoptera.

191

192 **Conclusion**

193 The present description of the new family Roqueiidae, for the genus *Roqueia* gen. nov., adds to
194 the impressive diversity of the superorder Archaeorthoptera in the Late Carboniferous.
195 Nevertheless, a phylogenetic analysis of the whole clade is more and more necessary to clarify
196 the relationships between the different groups inside.

197

198 **Acknowledgments**

199 We sincerely thank an anonymous referee, Dr. Jakub Prokop and Dr. Andrew Ross for their
200 useful comments on the first version of the paper.

201

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272

273 Figure 1. *Roqueia alpina* gen. et sp. nov. Nel & Duquesne, holotype. (A) Forewing Fa 0145b
274 (counterimprint), white arrowheads bases of posterior branches of MP; (B) Second forewing Fa
275 0145 (imprint), black arrowhead base of CuPb, white arrowhead MA. Scale bars = 10 mm.

276

277 Figure 2. *Roqueia alpina* gen. et sp. nov. Nel & Duquesne, holotype. (A) Fa 0145b
278 (counterimprint); (B) Fa 0145 (imprint), F.W. forewing, H.W. hind wing. Scale bars = 10 mm.



