



**HAL**  
open science

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

André Nel, Bruno Vallois, Hervé Duquesne

► **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-03566590v1>

Submitted on 11 Feb 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Historical Biology

2

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

4

5 Andre Nel<sup>a</sup>, Bruno Vallois<sup>b</sup> and Hervé Duquesne<sup>c</sup>

6

7 <sup>a</sup>Institut de Systématique, Évolution, Biodiversité (ISYEB) Muséum national d'Histoire  
8 naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 rue Cuvier, F-  
9 75005 Paris, France. [anel@mnhn.fr](mailto:anel@mnhn.fr); <https://orcid.org/0000-0002-4241-7651>

10 <sup>b</sup>Conservation Paléontologie et Paléobotanique, Muséum d'Histoire Naturelle de Grenoble,  
11 Grenoble, France. [bruno.vallois@wanadoo.fr](mailto:bruno.vallois@wanadoo.fr); <https://orcid.org/xxxx>

12 <sup>c</sup>App. 1, résidence Aronio de Romblay, 40 rue Jules Bedard, F-62800 Lievin, France.  
13 [hduquesne@wanadoo.fr](mailto:hduquesne@wanadoo.fr); <https://orcid.org/0000-0001-9785-6291>

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 $\beta$  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

## 202 **References**

203 Aristov DS. 2000. A new family of early Permian grylloblattids (Insecta: Grylloblattida) from  
204 the Ural Mountains. *Far Eastern Entomologist* **85**:1–4.

205 Aristov DS. 2013. New and little-known Eoblattida (Insecta) from the Paleozoic of Russia.  
206 *Paleontological Journal* 47:272–282. <https://doi.org/10.1134/S0031030113030039>

207 Aristov DS. 2014. Classification of the order Cnemidolestida (Insecta: Perlidea) with  
208 descriptions of new taxa. *Far Eastern Entomologist* 277:1–46.

209 Béthoux O, Nel A. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister  
210 groups. *Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov.* *Zootaxa* 96:1–88.  
211 <https://doi.org/10.11646/zootaxa.96.1.1>

212 Béthoux O. 2005. Cnemidolestodea (Insecta): an ancient order reinstated. *Journal of Systematic*  
213 *Palaeontology* 3:403–408. <https://doi.org/10.1017/S147720190500163X>

214 Béthoux O, Nel A. 2005. Some Palaeozoic 'Protorthoptera' are 'ancestral' orthopteroids: major  
215 wing braces as clues to a new split among the 'Protorthoptera'. *Journal of Systematic*  
216 *Palaeontology* 2:1–25. <https://doi.org/10.1017/S1477201904001488>

217 Brongniart C. 1885. Les insectes fossiles des terrains primaires. Coup d'œil rapide sur la faune  
218 entomologique des terrains paléozoïques. *Bulletin de la Société des Amis des Sciences*  
219 *Naturelles de Rouen* (3) **21**:50–68.

220 Dvořák T, Pecharová M, Krzemiński W, Prokop J. 2019. New archaeorthopteran insects from  
221 the Carboniferous of Poland: insights into tangled taxonomy. *Acta Palaeontologica Polonica*  
222 64:787–796. <https://doi.org/10.4202/app.00614.2019>

223 Dvořák T, Pecharová M, Leipner A, Nel A, Prokop J. 2021. New archaeorthopteran insects  
224 from the Pennsylvanian of Piesberg reveal unexpected mosaic of morphological traits and  
225 colouration pattern of the tegmina. *Historical Biology*,  
226 <https://doi.org/10.1080/08912963.2020.1867127>

227 Gu J-J, Béthoux O, Ren D. 2011. *Longzhua loculata* n. gen. n. sp., one of the most completely  
228 documented Pennsylvanian Archaeorthoptera (Insecta; Ningxia, China). *Journal of*  
229 *Paleontology* 85:303–314. <https://doi.org/10.1666/10-085.1>

230 Gu J-J, Béthoux O, Ren D. 2014. A new cnemidolestodean stem-orthopteran insect from the  
231 Late Carboniferous of China. *Acta Palaeontologica Polonica* 59:689–696.  
232 <https://doi.org/10.4202/app.2011.0204>

233 Handlirsch A. 1911. New Paleozoic insects from the vicinity of Mazon creek, Illinois.  
234 *American Journal of Science* 31:297–326 + 353–377. [https://doi.org/10.2475/ajs.s4-](https://doi.org/10.2475/ajs.s4-31.185.353)  
235 [31.185.353](https://doi.org/10.2475/ajs.s4-31.185.353).

236 Handlirsch A. 1937. Neue Untersuchungen über die fossilen Insekten. *Annalen des*  
237 *Naturhistorischen Museums in Wien* 48:1–140. <https://www.jstor.org/stable/41768379>

238 Langiaux J, Parriat H. 1974. Faune entomologique du bassin de **Blanzay-Montceau**. *La*  
239 *Physiophile* 81:62–74.

240 Martins-Neto RG, Gallego OF, Brauckmann C, Cruz JL. 2007. A review of the South American  
241 Palaeozoic entomofauna. Part I: the Ischnoneuroidea and Cacurgoidea, with description of  
242 new taxa. *African Invertebrates* 48:87–101. <https://hdl.handle.net/10520/EJC84588>

243 Nel A, Poschmann MJ. 2021. A new representative of the ‘orthopteroid’ family  
244 Cnemidolestidae (Archaeorthoptera) from the Early Permian of Germany. *Acta*  
245 *Palaeontologica Polonica* 66:641–646. <https://doi.org/10.4202/app.00879.2021>

246 Pinto, I.D. and Pinto de Ornellas, L. 1980. Upper Carboniferous insects from Argentina. 2.  
247 Familia Narkemocacurgidae (Paraplecoptera). Boletín de la Academia Nacional de Ciencias  
248 de Córdoba 53:287–291.

249 Schubnel T, Desutter-Grandcolas L, Legendre F, Prokop J, Mazurier A, Garrouste R,  
250 Grandcolas P, Nel A. 2020. To be or not to be: postcubital vein in insects revealed by  
251 microtomography. Systematic Entomology 45:327–336. <https://doi.org/10.1111/syen.12399>

252 Schubnel T, Legendre F, Roques P, Garrouste P, Cornette R, Perreau M, Perreau N, Desutter-  
253 Grandcolas L, Nel A. 2021. Sound vs. light: wing-based communication in Carboniferous  
254 insects. Communications Biology 4 (794):1–11. [https://doi.org/10.1038/s42003-021-02281-](https://doi.org/10.1038/s42003-021-02281-0)  
255 0

256 Schubnel T, Roberts D, Roques P, Garrouste R, Desutter-Grandcolas L, Nel A. 2019.  
257 Moscovian fossils shed light on the enigmatic polyneopteran families Cacurgidae and  
258 Eoblattidae (Insecta: ‘Eoblattida’, Archaeorthoptera). Journal of Systematic Palaeontology  
259 18:499–511. <https://doi.org/10.1080/14772019.2019.1627595>

260 van Beneden P-J, Coemans E. 1867. Un insecte et un gastéropode pulmoné du terrain houiller.  
261 Bulletin de l'Académie Royale de Belgique (2) 23:384–401.

262 Wagner RH, Álvarez-Vázquez C. 2010. A redescription of the Stephanian species  
263 *Callipteridium virginianum* (Fontaine & White, 1880) comb. nov. and *Alethopteris leonensis*  
264 Wagner, 1964. Scripta Geologica Special Issue 7:93–139.

265 Whalley PES. 1979. New species of Protorthoptera and Protodonata (Insecta) from the Upper  
266 Carboniferous of Britain, with a comment on the origin of wings. Bulletin of the British  
267 Museum of Natural History Geology 32:85–90. [http://creativecommons.org/licenses/by-nc-](http://creativecommons.org/licenses/by-nc-sa/4.0/)  
268 [sa/4.0/](http://creativecommons.org/licenses/by-nc-sa/4.0/)



269 Wittry J, Glasspool IJ, Béthoux O, Koll R, Cleal, CJ. 2014: A revision of the Pennsylvanian  
270 marattialean fern *Lobatopteris vestita* auct. and related species. Journal of Systematic  
271 Palaeontology 13:615–643. <https://doi.org/10.1080/14772019.2014.936915>

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.





