A new family and two new genera from Avion, Northern France, confirm the high Moscovian (late Carboniferous) diversity of the insect superorder Archaeorthoptera

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The new archaeorthopteran family Archaeogeraridae, based on *Archaeogerarus schubneli* gen. et sp. nov., is described from the Moscovian of Avion. It has several unique wing venation characters allowing to separate it from the other groups of this superorder, viz. a vein RP separating from RA very close to wing base and closely parallel to it; M shortly fused with RP; CuA+CuPa simple and straight; and CuPb branched. This last character is convergently present in a few Palaeozoic Panorthoptera, a feature of great interest for a future phylogenetic analysis of the whole superorder. *Avionxixia gui* gen. et sp. nov., second Cnemidolestidae from the Moscovian of Avion, is described and illustrated. It shares numerous characters with the Chinese Namurian genus *Xixia* and the European (Germany and France) Moscovian genus *Piesbergopterum*, suggesting possible phylogenetic affinities between these three genera. It is mainly separated from these two genera by the costal area much narrower than the subcostal one and the presence of only one posterior branch of the anterior branch of MP+CuA+CuPa. This new taxon confirms the high diversity of the Cnemidolestidae during the late Carboniferous.

Key words: Insecta, Polyneoptera , Cnemidolestodea, Archaeogeraridae, forewing venation convergences, Carboniferous, France.

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Introduction

The superorder Archaeorthoptera, now-a-day reduced to the sole Orthoptera, witnesses an impressive diversification during the Palaeozoic and the early Mesozoic, with the orders Caloneurodea, Titanoptera, Cnemidolestodea, stem Orthoptera and a complex series of families and genera belonging to the Archaeorthoptera nec Panorthoptera (Béthoux and Nel 2002). Some historical outcrops have given numerous fossils of this superorder (e.g., Mazon Creek, USA; Commentry, France), showing that it was probably among the most diverse clade during the late Carboniferous, together with the two other polyneopteran groups Dictyoptera and "Grylloblattodea". But, if the Dictyoptera were clearly very abundant, their morphological disparity was clearly lower than that of the Archaeorthoptera. That of the "Grylloblattodea" was very high too, but the monophyly of this group of taxa remains to be verified, unlike that of the Archaeorthoptera, well supported by a series of wing venation synapomorphies. Thanks to the efforts of one of us (PR), the Moscovian outcrop of Avion (Northern France) has given recently an impressive series of fossil insects, among which were found the oldest representatives of the Acercaria and Holometabola (Nel et al. 2013), but also numerous Archaeorthoptera of several orders and families. Nevertheless, all these new genera and species are based on single fossils, suggesting that the diversity of the original entomofauna was much higher than what has been recovered.

The present descriptions of two new fossils representing a new family, and two new genera and species support this assumption. They are of great interest for a better knowl-

edge of the Moscovian diversity and morphological disparity of the Archaeorthoptera.

Institutional abbreviations.—MNHN, Muséum National d'Histoire Naturelle, Paris, France.

Other abbreviations.—A, anal vein; C, costa; CuA, cubitus anterior; CuP, cubitus posterior; CuPa, anterior branch of CuP; CuPaa, anterior branch of CuPa; CuPab, posterior branch of CuPa; CuPb, posterior branch of CuP; MA, median anterior vein; MP, median posterior vein; PCu, postcubital vein; RA, radius anterior; RP, radius posterior; ScP, subcostal posterior.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:7D23AD1B-CA20-4BB8-A926-CEE97C49ADF1

Material and methods

The fossils were found by one of us (PR) in the slag heap of Avion. They were examined and drawn under a Nikon SMZ1500, and photographed with an AmScope camera MU900.

We follow the wing venation terminology of Béthoux and Nel (2002) modified by Schubnel et al. (2020), and the classification of Béthoux (2005) for the Cnemidolestodea.

Systematic palaeontology

Superorder Archaeorthoptera Béthoux and Nel, 2002

Order undetermined

Family Archaeogeraridae nov.

Zoobank LSID: urn:lsid:zoobank.org:act:5283533C-1641-4366-A77D-5CADECB66536

Type genus: *Archaeogerarus* gen. nov.; see below.

Diagnosis.—As for the type genus by monotypy.

Genus *Archaeogerarus* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:95D9C644-779C-440E-BBCC-71D6846D3D40

Type species: *Archaeogerarus schubneli* sp. nov.; see below.

Etymology: From Ancient Greek ἀρχαῖος (arkhaîos), primitive, and the genus *Gerarus* for its similarity in the forewing vein CuPb (gender masculine).

Diagnosis.—As for the type species by monotypy.

Archaeogerarus schubneli sp. nov.

Fig. 1.

Zoobank LSID: urn:lsid:zoobank.org:act:81243C11-E3B1-4DF4-9561-C0E248E23A41

Etymology: In honour of Thomas Schubnel, for his impressive scientific activity and the very useful interactions we have in the study of extant and fossil insect wing venation.

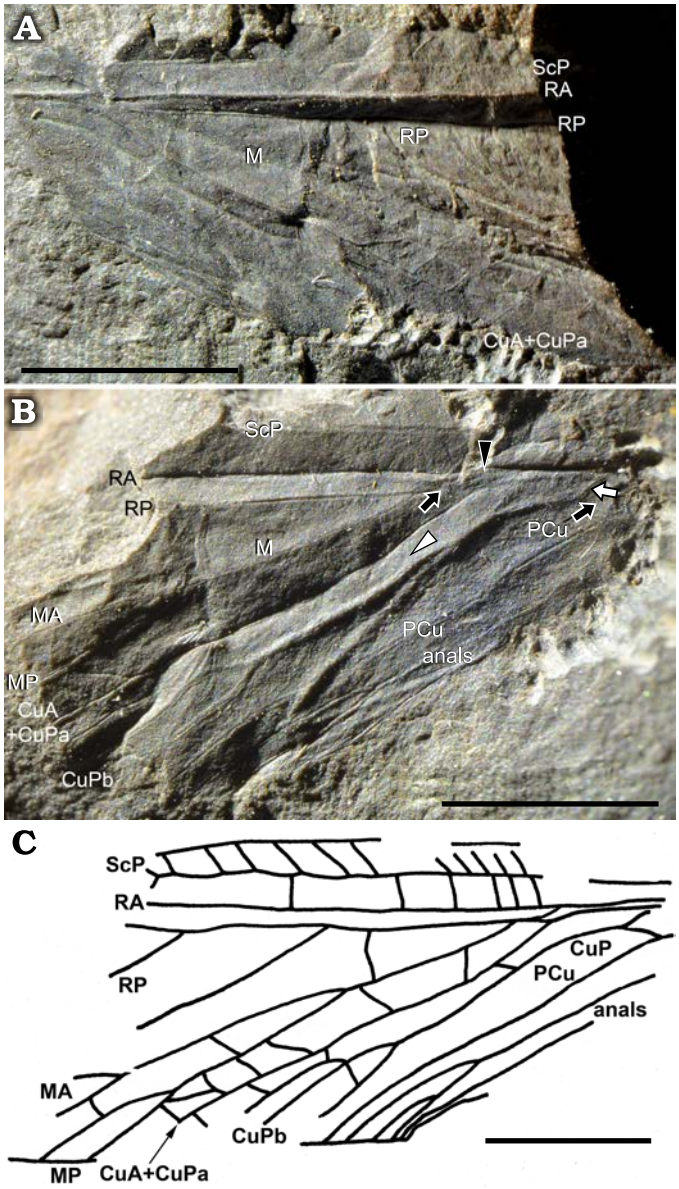

Fig. 1. Archaeorthopteran insect *Archaeogerarus schubneli* gen. et sp. nov., holotype MNHN.F.A70991 from Avion, France, Moscovian. Forewing, part (**A**) and counterpart (**B**) (photographs Thomas Schubnel), reconstruction (**C**). Black arrowhead, base of RP; white arrowhead, CuPa; black arrows, point of fusion between RP and M; white arrow, base of CuP. Scale bars 4 mm.

Holotype: MNHN.F. A70991, part and counterpart of the basal half of a forewing, with polarity of veins well visible.

Type locality: Terril N°7, Avion, Pas-de-Calais, France.

Type horizon: Moscovian (Westphalian C/D equivalent to Bolsovian/Asturian), middle Pennsylvanian, Carboniferous.

Material.—Type material only.

Diagnosis.—Forewing characters only. Base of RP opposite point of separation of M and CuA; RP closely parallel with RA; M shortly fused with RP and separating again distally (autapomorphy); CuA+CuPa simple (autapomorphy); CuPa very short; CuPb (+ first branch of PCu) with elongate distal branches; second branch of PCu simple; first anal vein with elongate branches; second anal vein elongate and sim-

ple. Further characters: ScP ending into C; CuP with three branches; M with four branches.

Description.—Based on forewing venation. Length of preserved part 17.0 mm, maximum width at midwing 7.5 mm; original coloration of wing membrane not preserved or hyaline; concave ScP distally slightly zigzagged, running parallel with costal margin, not ending into RA; costal area with numerous simple crossveins, 0.6 mm wide, slightly narrower than subcostal area, 0.8 mm wide; stem of R diverging from M+CuA near base of wing; division of RA and RP very basal, opposite point of separation of M and CuA, less than 1.0 mm distal of point of separation of R and M+CuA; strongly convex RA simple; concave RP very closely parallel with RA and with at least two posterior branches; neutral vein M diverging from M+CuA very close to its base, parallel to R, shortly fused with RP, and separating again 0.2 mm distally; M divided into MA and MP 4.5 mm distal to its separation from RP; both MA and MP with a distal fork; concave vein CuPa very short, ending into convex CuA 2.0 mm behind divergence of M from CuA; convex CuA+CuPa straight and simple (even if there are several oblique crossveins between it and MP superficially looking like anterior branches of CuA+CuPa); elongate concave CuP basally strongly curved towards R+M+CuA, CuPb with three long branches; a convex vein (anterior branch of PCu) separating from PCu at its base and ending into CuP; anal area with simple convex vein PCu 9.8 mm long, running parallel to CuP and CuPb; a broad area between CuP/CuPb and PCu; first anal vein with three branches; a second simple anal vein; no anal loop.

Remarks.—*Archaeogerarus* gen. nov. can be clearly attributed to the Archaeorthoptera as it shares the main diagnostic character of this superorder, namely the basal fusion of CuA with M and subsequent connection with the concave anterior branch of CuP as CuPa (Béthoux and Nel 2002). The absence of a division of CuPa into two branches CuPaa and CuPab is a symplesiomorphy excluding it from the Panorthoptera sensu Béthoux and Nel (2002). The most remarkable characters of *Archaeogerarus* gen. nov. is the vein RP closely parallel to RA and branching from R opposite the point of separation of M and CuA, and the vein M directly ending into RP to separate again just distally. A RP very long and closely parallel to RA is present in some Anthracoptilidae (in Palaeozoic order Paoliida), e.g., *Mesoptilus dolloi* Lameere, 1917 (Guan et al. 2015); but these have a completely different pattern of the median and cubital veins at wing base, with a stem Cu from which the convex CuA and the concave CuP distally emerge. Such a vein RP elongate and closely parallel to RA, is also present in few Archaeorthoptera, viz. *Eoblatta robusta* (Brongniart, 1893), *Beloatta duquesnei* Nel, Garrouste, and Roques, 2020, *Ctenoptilus elongatus* (Brongniart, 1893), *Ischnoneura oustaleti* Brongniart, 1893, *Ischnoptera diaphanes* Béthoux and Nel, 2005, *Kitshuga ryzhkovae* Aristov, 2012 (Béthoux and Nel 2005; Schubnel et al. 2019). All these taxa strongly differ from *Archaeogerarus* gen. nov. in the CuA+CuPa with numerous strong branches vs. simple in *Archaeogerarus schubneli* gen. nov., M not fused with RP near their bases, and CuPb simple vs. with branches in *Archaeogerarus schubneli* gen. nov.

In the other polyneopteran orders, the vein CuP is simple, suggesting that that a branched CuPb is a specialized structure of some Archaeorthoptera. It is encountered in very few Archaeorthopteran Panorthoptera, viz. *Gerarus bruesi* Meunier, 1909, *Owadpteron dareki* Dvořák, Pecharová, Krzemiński, and Prokop, 2019, and *Nacekomia rossae* Richardson, 1956 (Béthoux and Nel 2002; Dvořák et al. 2019). But these have a branched CuPa into a CuPaa and a CuPab (as Panorthoptera), and a branched CuA+CuPaa, unlike *Archaeogerarus schubneli* gen. nov. *Archaeogerarus* gen. nov. is the first Archaeorthoptera not belonging to the Panorthoptera with a branched CuPb. This character is a putative convergence between it and the panorthopteran genera *Gerarus*, *Owadpteron*, and *Nacekomia*. Notice that the pattern of PCu and of the anal veins of *Archaeogerarus schubneli* gen. nov. is similar to that of *Nacekomia rossae*, these veins being very long and parallel.

The presence of this unique combination of characters plus some extremely particular structures supports the attribution of *Archaeogerarus schubneli* gen. et sp. nov. to a new family of Archaeorthoptera.

Stratigraphic and geographic range.—Type locality and horizon only.

Order Cnemidolestodea Handlirsch, 1937 (sensu Béthoux 2005)

Family Cnemidolestidae Handlirsch, 1906

Genus *Avionxixia* nov.

Zoobank LSID: uurn:lsid:zoobank.org:act:2494907A-6BFE-4FCC-97CA-E615D573272D

Type species: *Avionxixia gui* sp. nov.; see below.

Etymology: Named after the type locality Avion and the genus *Xixia*.

Diagnosis.—As for the type species by monotypy.

Avionxixia gui sp. nov.

Fig. 2.

Zoobank LSID: urn:lsid:zoobank.org:pub:7D23AD1B-CA20-4BB8-A926-CEE97C49ADF1

Etymology: Named after Jun-Jie Gu, for his work on the Cnemidolestidae.

Holotype: MNHN.F. A70990, part and counterpart of a nearly complete forewing, with only apex missing.

Type locality: Terril N°7, Avion, Pas-de-Calais, France.

Type horizon: Moscovian (Westphalian C/D equivalent to Bolsovian/Asturian, middle Pennsylvanian, Carboniferous).

Material.—Type material only.

Diagnosis.—Forewing characters only. Only one posterior branches of anterior branch of MP+CuA+CuPa; veinlet between MP+CuA+CuPa and posterior branch of MA strongly zigzagged and very short; area between MA and

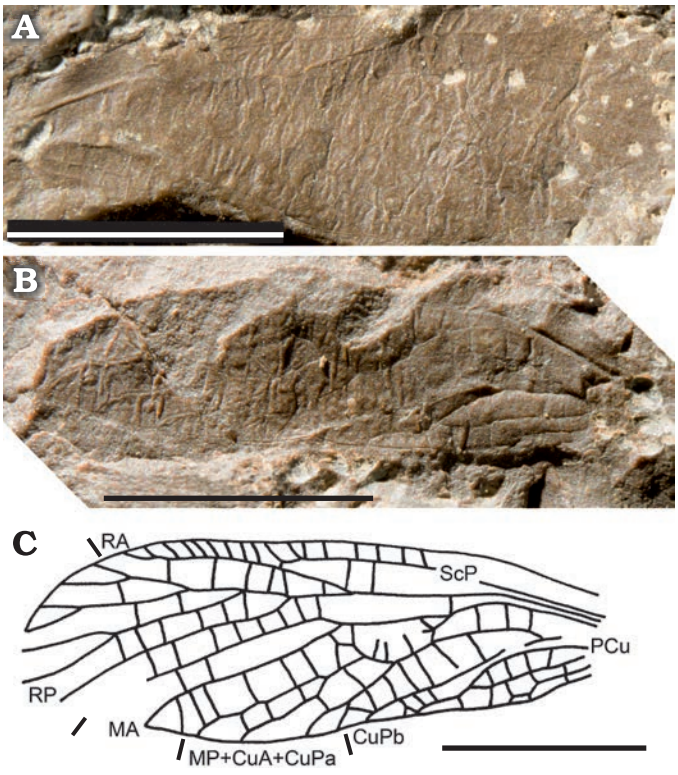

Fig. 2. Archaeorthopteran insect *Avionxixia gui* gen. et sp. nov., holotype MNHN.F.A70990 from Avion, France, Moscovian. Forewing, photograph of imprint (**A**) and counterimprint (**B**), reconstruction (**C**). Scale bars 4 mm.

anterior branch of MP+CuA+CuPa quite short, less than three times as long as wide; anterior branch of MA not touching RP; costal area distinctly narrower than subcostal area. Forewing only 12.1 mm long.

Description.—Based on forewing venation. Estimated total wing length 12.1 mm, maximum width at midwing 4.1 mm; bending of costal margin in about basal third; original coloration of wing membrane not preserved or hyaline; concave ScP slightly curved, running parallel with costal margin, ending to RA behind midwing; costal area with numerous simple crossveins, 0.3 mm wide, narrower than subcostal area, 0.6 mm wide; stem of R diverging from M+CuA near base of wing; division of RA and RP proximal of midwing, 1.5 mm basal to connection of ScP on RA; strongly convex RA simple ending on costal margin well basal to wing apex; numerous oblique crossveins present in space between RA and costal wing margin; concave RP posteriorly pectinate ending with four branches covering whole distal part of wing; neutral vein MA diverging from M+CuA and further running parallel to stem of R/RP; MA deeply forked into two simple branches, anterior one MA1 not connected to RP and posterior one MA2 nearly straight; concave vein CuPa ending into MP+CuA shortly behind divergence of MA from MP+CuA; MP+CuA+CuPa emitting a posterior branch apically subdivided into two branches; and an anterior branch parallel to MA, emitting only one posterior branch, distally forked, a strongly zigzagged veinlet between MP+CuA+CuPa and MA, closing a short and broad area between it and MA (0.8 mm wide, 2.0 mm long), crossed by irregular veinlets; areas between branches of RP, MA and MP+CuA+CuPa regularly connected by simple and oblique crossveins; concave CuP basally dividing into CuPa and CuPb, simple CuPb running parallel to MP+CuA+CuPa towards posterior wing margin; anal area with convex vein PCu running parallel to CuP and CuPb; first anal vein distally connected to PCu, forming an elongate "anal loop", 2.5 mm long; a second short anal vein.

Remarks.—*Avionxixia* gen. nov. can be attributed to the Archaeorthoptera as it shares the main diagnostic character of this superorder, namely the basal fusion of CuA with M and subsequent connection with the anterior branch of CuP as CuPa (Béthoux and Nel 2002). Furthermore, it displays characters typical of the order Cnemidolestodea, such as ScP terminating on RA, CuPa ending into MP+CuA, MP+CuA+CuPa emitting an anterior branch parallel to MA, with a specialised veinlet between it and MA, thus defining a large area between it and MA crossed by irregular veinlets (Béthoux 2005; Gu et al. 2014: figs. 1, 2). Aristov (2014), using a different diagnosis and wing venation nomenclature for the Cnemidolestodea, proposed a key to families.

Avionxixia gen. nov. falls in the family Cnemidolestidae Handlirsch, 1906 (sensu Aristov 2014: 10) because of the character "MP weak, ending on CuA or MA, or absent". Indeed, in *Avionxixia* gen. nov., MP is clearly basally fused with CuA.

The family Cnemidolestidae comprises the following genera, after Aristov (2014), Gu et al. (2014), and Dvořák et al. (2021): *Aetophlebia* Scudder, 1885, *Amphiboliacridites* Langiaux and Parriat, 1974, *Anarkemina* Aristov, 2014, *Argentinonarkemina* Martins-Neto, Gallego, and Brauckmann, 2007, *Bouleites* Lameere, 1917, *Carbonokata* Aristov, 2013, *Cnemidolestes* Handlirsch, 1906, *Evenkiophlebia* Aristov, 2013, *Irajanarkemina* Martins-Neto, Gallego, and Brauckmann, 2007, *Ischnoneura* Brongniart, 1893, *Longzhua* Gu, Béthoux, and Ren, 2011, *Narkema* Handlirsch, 1911, *Narkemina* Martynov, 1930, *Narkeminopsis* Whalley, 1979, *Narkeminuta* Aristov, 2013, *Narkemulla* Aristov, 2013, *Paranarkemina* Pinto and Ornellas, 1980, *Piesbergopterum* Dvořák, Pecharová, Leipner, Nel, and Prokop, 2021, *Protodiamphipnoa* Brongniart, 1885, *Tshunoptera* Aristov, 2013, *Velizphlebia* Martins-Neto, Gallego, and Brauckmann, 2007, and *Xixia* Gu, Béthoux, and Ren, 2014.

Narkema (*N. taeniatum* Handlirsch, 1911, *N. alternatum* Cockerell, 1924) shares with *Avionxixia* gen. nov. the presence of only two posterior branches of anterior branch of MP+CuA+CuPa, but it has a very long stem of RP, a very long stem of anterior branch of MP+CuA+CuPa, and posterior branch of MP+CuA+CuPa branched (Handlirsch 1911: fig. 28; Cockerell 1924, 1927).

Irajanarkemina, *Velizphlebia*, *Argentinonarkemina*, and *Paranarkemina* have few or no posterior branch of the anterior branch of MP+CuA+CuPa, but they all have a longer stem of RP and a narrower area between MA and MP+CuA+CuPa than in *Avionxixia* gen. nov. *Aetophlebia* and *Longzhua* also differ from *Avionxixia* gen. nov. in the

Table 1. List of genera and species of Archaeorthoptera from Avion, France.

Major clade	Family, order	Species
Archaeorthoptera nec Panorthoptera	?Nugonioneuridae	*Avionugonioneura jouaulti* Nel and Roques, 2021a
	Archaeogeraridae	*Archaeogerarus schubneli* gen. et sp. nov.
	Cnemidolestidae	*Avionxixia gui* gen. et sp. nov.
		Piesbergopterum avionensis Nel and Roques, 2021c
		Aviocladus pectinatus Prokop, Roques, and Nel, 2014
		Aviohapaloptera bethouxi Prokop, Roques, and Nel, 2014
		Tococladus sp. (Coty, Háva, Prokop, Roques, and Nel, 2014)
Panorthoptera	Caloneurodea	*Aviobiella garrousti* Nel and Roques, 2021b
		Aviogramma gracilis Prokop, Roques, and Nel, 2014
	Titanoptera	*Theiatitan azari* Schubnel, Roques, and Nel, 2021
	Cacurgidae	*Cacurgus avionensis* Schubnel, Roberts, Roques, Garrouste, Desutter-Grandcolas, and Nel, 2019
	Eoblattidae	*Beloatta duquesnei* Nel, Garrouste, and Roques, 2020
	Family undetermined	*Aviologus duquesnei* Coty, Háva, Prokop, Roques, and Nel, 2014

same characters (Scudder 1890: 301–302, pl. 17: 9; Martins-Neto et al. 2007: figs. 2, 7; Gu et al. 2011: fig 3). *Avionxixia* gen. nov. differs from *Narkeminopsis* in much broader area between MA and MP+CuA+CuPa (Whalley 1979: fig. 3; Brauckmann and Herd 2006: fig. 9; Béthoux and Nel 2005: fig. 20; Aristov 2013: fig. 1b).

Piesbergopterum (*Piesbergopterum punctatum* Dvořák, Pecharová, Leipner, Nel, and Prokop, 2021, *Piesbergopterum schubneli* Nel and Roques, 2021c), and *Xixia* (*Xixia huban* Gu, Béthoux, and Ren, 2014) share with *Avionxixia* gen. nov. the presence of few posterior branches of anterior branch of MP+CuA+CuPa (two or three at most) (Gu et al. 2014; Dvořák et al. 2021; Nel and Roques 2021c). The specialized veinlet between MP+CuA+CuPa and posterior branch of MA is short and simple in *Piesbergopterum*, vs. elongate and more or less sigmoidal with crossvein(s) branching on it in *Xixia*. In *Avionxixia* gen. nov., this veinlet is strongly zigzagged and very short. *Piesbergopterum* has a posterior branch of MP+CuA+CuPa with more than two branches, unlike *Avionxixia* gen. nov. and *Xixia*. Lastly, the area between MA and anterior branch of MP+CuA+CuPa is quite short in *Avionxixia* gen. nov., less than three times as long as wide, while it is three times (or more) as long as wide in *Xixia* and *Piesbergopterum*. The anterior branch of MA in *Avionxixia* gen. nov. is not touching RP, unlike in *Piesbergopterum*. The costal area of *Avionxixia* gen. nov. is distinctly narrower than the subcostal area, unlike in *Piesbergopterum* and *Xixia*. Lastly the forewing of *Avionxixia* gen. nov. is only 12.1 mm long, instead of 20–21 mm in the two species of *Piesbergopterum*, and 17.9–21.8 mm in *Xixia huban*.

All the other cnemidolestid genera have three or more posterior branches of the anterior branch of MP+CuA+CuPa, which is itself quite elongate, unlike *Avionxixia* gen. nov.

It is worth to note that apart from *Piesbergopterum avionensis* there are two other cnemidolestodeans known from Avion: *Avionxixia gui* gen. nov. differs strongly both from *Aviocladus pectinatus* Prokop, Roques, and Nel, 2014 and *Aviohapaloptera bethouxi* Prokop, Roques, and Nel, 2014 in the presence of a strong anterior branch of MP+CuA+CuPa and the different shape of CuA+CuPa (Prokop et al. 2014).

Stratigraphic and geographic range.—Type locality and horizon only.

Concluding remarks

With these two new taxa, the Avion locality shows an impressive diversity of Archaeorthoptera, with no less than 13 genera and 13 species (Table 1; 10% of the ca. 121 Carboniferous archaeorthopteran species, after the Fossilworks Database http://fossilworks.org accessed 30/08/2021). It confirms that this superorder underwent an important diversification during the late Carboniferous, with a high disparity of wing venations. Unfortunately no body structure of these insects has been found in Avion, which is also rarely encountered in the other Carboniferous outcrops. Thus their biology remains unknown in main part. The discovery of *Archaeogerarus schubneli* gen. et sp. nov. with a highly specialized branched vein CuPb, convergently present in a few Panorthoptera, is especially interesting for a future phylogenetic analysis of the whole superorder Archaeorthoptera.

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