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A new 'grylloblattodean' genus and species (Insecta: Polyneoptera) from the middle Permian Salagou Formation (France)

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Abstract. *Lodevoisadia coheni* gen. et sp. nov. is described as the ninth species of 'Grylloblattodea' from the middle Permian of the Salagou Formation, near Lodève town (France). It is currently not reasonable to place this species into a specific family, even though it seems to share most characters with the small family Tunguskapteridae. The lack of phylogenetic analysis and the current poor delineation of the majority of the grylloblattodean families (lacking synapomorphies) render any attribution of new taxa to a particular family often uncertain.

Keywords. Grylloblattida, classification, lack of phylogenetic analysis, taxonomy.

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Introduction

The fossil 'Grylloblattodea' Brues & Melander, 1932 is assumed to be the stem group of the extant apterous order Grylloblattida Walker, 1914 (see Storozhenko 1998; Aristov 2015). To date, there is still no evidence (synapomorphy) supporting these relationships and even the monophyly of the 'Grylloblattodea', because there is no phylogenetic analysis of the whole extant and fossil Polyneoptera Martynov, 1938. Nevertheless, this group is known from numerous winged fossils from late Carboniferous to mid-Cretaceous deposits. The current compositions and delineations of the families placed in the 'Grylloblattodea' are poorly justified, due to the lack of phylogeny. This 'clade' is subdivided into a number of families generally not supported by clear synapomorphies. Therefore, the systematics of this 'lineage' is very confusing, despite several attempts at reclassification (e.g., Storozhenko 1998; Aristov 2015). The 'grylloblattodeans' are especially frequent and speciose in Permian outcrops, sometimes more than the Dictyoptera Leach, 1815 (Cawood *et al.* 2022), otherwise also very speciose and frequent in Carboniferous deposits.

The middle Permian of the Salagou Formation (near Lodève town, Southern France) has yielded an impressive diversity of fossil insects, with 14 orders recorded (Prokop & Nel 2011; Prokop *et al.* 2014, 2015a, 2015b; Szwedo *et al.* 2015; Garrouste *et al.* 2018; Nel *et al.* 2019). The superorder Archaeorthoptera Béthoux & Nel, 2002 is especially diverse (see list in Prokop *et al.* 2015b). Among this rich paleoentomofauna, the 'Grylloblattodea' are represented by eight species, viz. *Lodevopterum angustus* Béthoux *et al.*, 2005, *Depressopterum minutus* Béthoux *et al.*, 2005, two liomopterid genera and species undetermined, *Permobaharellus salagousensis* Prokop *et al.*, 2015, *Lodevophlebia reticulata* Prokop *et al.*, 2015, *Oborella lodevensis* Prokop *et al.*, 2015, and a 'Grylloblattodea' genus and species undetermined. Nevertheless, the diversity of the group is still underestimated, and we describe here a new genus and species quite different from those previously found, especially because of its simple RP and MA and its simply forked MP.

Material and methods

Origin, preparation and examinations

Pfeifer *et al.* (2020) proposed an age between 285 and 262 Ma for the whole Salagou Formation. 'Les Canals' level from which the fossil originated belongs to the 'Mérifons member', likely dating from the late Kungurian (272–277 Ma). It is younger than the early Kungurian of Octon and older than the late Roadian of La Lieude (Pfeifer *et al.* 2020: fig. 2).

The type specimen was collected by Henri Cohen in 2004. The specimen was prepared with a very sharp pneumatic needle and studied using a stereo microscope Olympus SCX9. Photographs were taken with a Nikon SMZ 25 stereo microscope with an attached Nikon D800 camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus. The figures were composed with Adobe Illustrator and Adobe Photoshop CC2019 software.

Wing venation abbreviations

The nomenclature of the wing venation generally follows the scheme employed by Béthoux *et al.* (2005).

AA1 and AA2	=	anal vein
C	=	costa
CuA/CuP	=	cubitus anterior/posterior
MA/MP	=	media anterior/posterior
m-cua	=	arculus crossvein between M and CuA.
RA/RP	=	radius anterior/posterior
ScP	=	subcosta posterior

Results

Clade Polyneoptera Martynov, 1938
Order 'Grylloblattodea' Brues & Melander, 1932
Family Incertae sedis

Genus ***Lodevoisadia*** gen. nov.
urn:lsid:zoobank.org:act:CB082E08-C310-4BBD-ACE8-FEFA3D7DC580

Type species

Lodevoisadia coheni gen. et sp. nov.

Diagnosis

Costal area narrow; ScP ending into C; RP simple; MA simple; MP forked; CuA1 with three branches; CuA2 simple; arculus m-cua present between M and CuA1; areas between RA and RP, RP and MA, and between MA and MP distally widened; few simple crossveins between RP, MA, and MP.

Etymology

The genus name is a combination of the town of Lodève and the genus name *Isadia*. Gender feminine.

Lodevoisadia coheni gen. et sp. nov.
urn:lsid:zoobank.org:act:59BE288B-C752-4898-ACE5-72799793A9F6
Fig. 1

Diagnosis

As for the genus (vide supra).

Etymology

Named after Henri Cohen, who discovered the type specimen and allowed us to study it. The specific epithet is to be treated as a noun in genitive case.

Type material

Holotype

Specimen 2022.3.2 (number HC Can 01a-b, part and counterpart of a forewing, collection Henri Cohen); Musée of Lodève, France.

Description

Counterpart of an almost complete right forewing, with costal part of extreme base not preserved, 10.4 mm long (as preserved), ca 3.5 mm wide; area between C and ScP narrow, ca 0.2 mm wide; ScP simple, closely parallel to R, ending in C at 8.0 mm from wing base; few weak and short veinlets between RA and C near apex of RA; base of RP at 3.3 mm from wing base; RP simple; base of MP at 2.5 mm from wing base; MA simple; MP forked 3.3 mm distad origin of MP; crossveins in areas between RA and MP spaced; course of RP and MA nearly straight; areas between RA and RP and between RP and MA distally widened; CuA convex, with a nearly straight and simple basal posterior branch CuA2; CuA1 branched at 2.0 mm distad its base; area between MP and CuA1 rather broad basad first branch of CuA1; RP, M, and CuA well-separated; arculus m-cua present between M and CuA1; CuP concave, straight, and simple; AA1 and AA2 convex and simple.

Discussion

Following the key to grylloblattodean families of Storozhenko (1998), the new fossil would fall in the family Tunguskapteridae Storozhenko & Vršanský, 1995 because of the following combination of characters (adapted terminology): a strong arculus m-cua; ScP ending into C; M with two elongate main branches, completely separated from CuA; RP simple; a clear subdivision of CuA into CuA1 and CuA2. The type genus *Tunguskaptera* Storozhenko & Vršanský, 1995 (252.3 to 251.3 Ma, Russian Federation) shares with the new fossil a simple MA, but differs from it in the very long CuA1, surpassing the level of

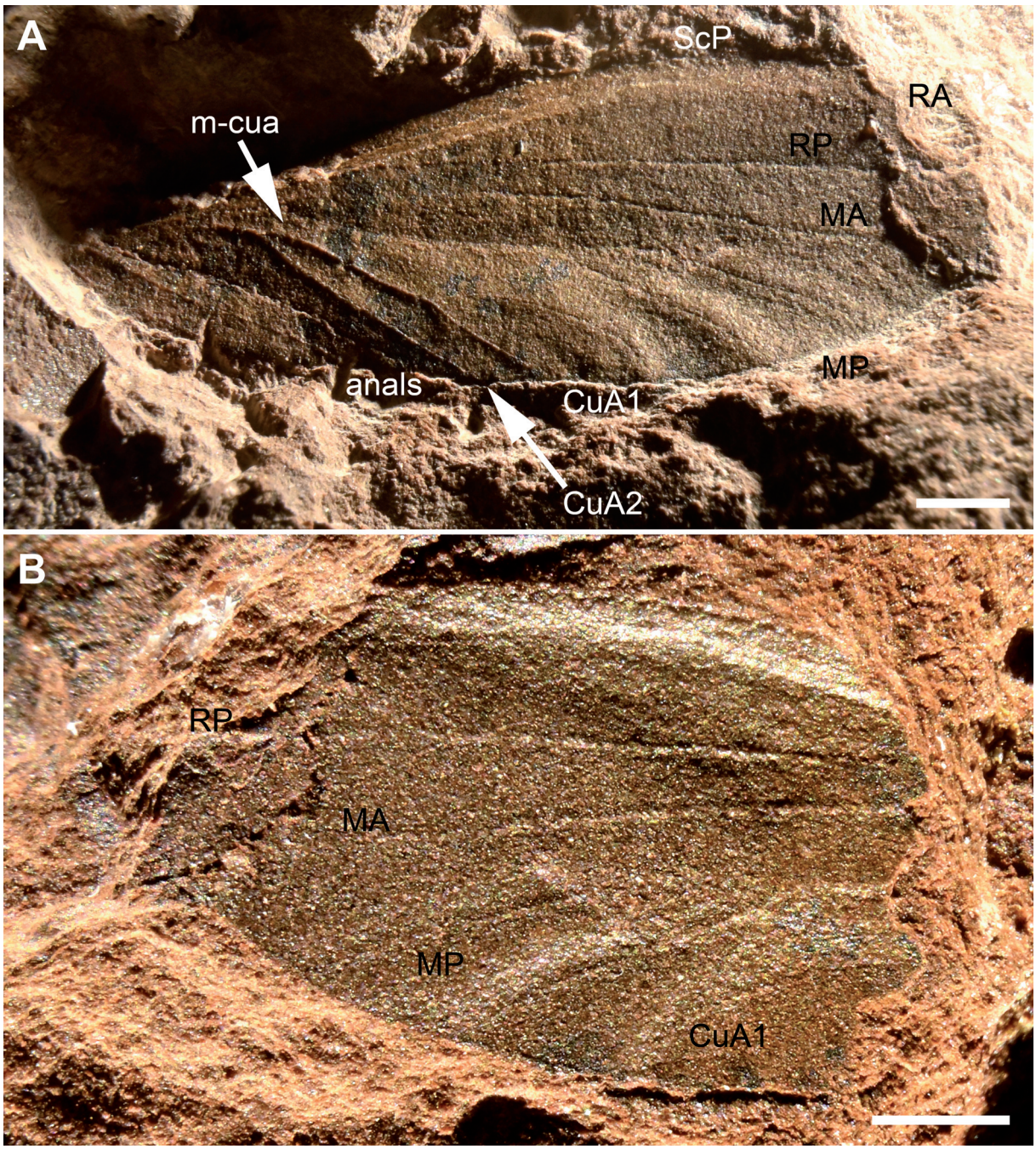

Fig. 1. *Lodevoisadia coheni* gen. et sp. nov., holotype 2022.3.2. Photographs. **A**. Part. **B**. Counterpart of wing apex. Scale bars = 1 mm.

the midwing, and in the simple MP (Storozhenko & Vršanský 1995). The tunguskapterid genus *Isadiella* Aristov, 2019 (replacement name for *Isadia* Aristov, 2009; 259.0 to 254.0 Ma, Wuchiapingian, Induan, Russian Federation) shares with the new fossil simple RP and MA, a forked MP, a CuP only reaching the level of base of RP, but it has a CuA1 terminating posteriad wing mid-length, and a very broad area between C and ScP with very long branches of ScP; *Tunguskaptera* also differs from *Isadiella* in having a narrow area between C and ScP (Aristov 2009).

The Necrophasmatidae Martynov, 1925 (= Juraperlidae Huang & Nel, 2007) (Aristov 2016, 2018) – including *Ferganamadygenia* Storozhenko & Vršanský, 1995 (originally in Tunguskapteridae, but transferred to the Juraperlidae by Aristov 2016) – share with the new fossil a simple RP and MA, but they have a simple MP, while forked in the new fossil (Huang & Nel 2007; Cui *et al.* 2010). Note that, they also possess a precostal area in their forewings, but we cannot confirm the presence of this character on the new fossil because the extreme base of the costal area is not preserved. *Ferganamadygenia* further differs from the new fossil in the very long anal area, with CuP reaching wing mid-length.

Some Euryptilonidae Martynov, 1940 (e.g., *Torrentopterum* Kukalová 1964, *Villopterum* Kukalová 1964, *Sharovipterum* Kukalová 1964) and Lemmatophoridae Sellards, 1909 (e.g., *Artinska infigurabilis* Aristov, 2004) also have a simple RP and few crossveins between mains veins, but they have at least a short anastomosis between M and CuA. Note that *Artinska infigurabilis* strongly differs from the type species of *Artinska* Sellards, 1909 because of its simple MP and CuA1 (Storozhenko 1998; Aristov 2004). The Probnidae Sellards, 1909 (e.g., *Probnis* Sellards, 1909) and the Sylvaphlebiidae Martynov, 1940 (e.g., *Sylvophenoptera* Aristov, 2004) have also a simple RP and a rather reduced anal area as in the new fossil, but they have a very long CuA1 (comparatively shorter in the new fossil). The Permembiidae Tillyard, 1937, Sheimiidae Martynova, 1958, Sojanoraphidiidae Tillyard, 1937, and Soyanopteridae Aristov & Rasnitsyn, 2011 also have a reduced wing venation pattern with a few main veins branched and a few crossveins, but they differ from the new fossil because of the fusions of RP, M, and/or CuA (Storozhenko 1998; Aristov & Rasnitsyn 2011).

Some Liomopteridae Sellards, 1909 (e.g., *Liomopterites festivus* Sharov, 1961), share with the new fossil similar wing venation patterns with a simple MA, a forked MP, shape of CuA, size and shape of CuP and anal area, but they differ from it in the forked RP and absence of the arculus. A contrario, *Mioloptera stuckenbergi* Riek, 1973 has a simple RP but a forked MA and a CuA1 very long and with much more branches than in the new fossil (Aristov & Mostovski 2013). Therefore, the number of branches of the main veins and their relative proportions greatly vary in the Liomopteridae. Some Bajanzhargalanidae Storozhenko, 1992 (e.g., *Nele* Ansorge, 1996) have a RP and a MA with only a very short apical fork, and a forked MP, but they differ from the new fossil in their very long CuA. The presence of an arculus on the new fossil is the most significant character allowing us to exclude affinities with these groups.

The other grylloblattodean families have an RP with more than two branches, excluding any affinities for the new fossil (Storozhenko 1998; Peng *et al.* 2005; Rasnitsyn *et al.* 2005; Huang *et al.* 2007; Cui 2012).

The genus *Lodevopterum* Béthoux *et al.*, 2005 shares with the new fossil a very long RP, a simple MA, and CuA1 with three posterior branches, but strongly differs from it in the apically forked RP (vs simple), the very narrow areas between RA and RP and between RP and MA (vs distally broadened), the very long MA (vs comparatively short), MP with four long branches (vs two in the new fossil), and the very long CuP and anal veins (Béthoux *et al.* 2005).

As detailed above, the consequent intrafamilial or even intrageneric variability in the number of branches of the main veins, together with the lack of phylogenetic analysis of the 'Grylloblattodea' render quite uncertain the limits of the different families.

For instance, Béthoux *et al.* (2005) considered *Lodevopterum* as a 'Grylloblattodea' of an uncertain family, but Aristov (2009: 646) put it in the Euremiscidae Zalessky, 1951, indicating that it has 'has venation typical of Euremiscidae and differs from *Euremisca* only in the four branches of MP (in *Euremisca*, MP is simple or with two branches)'. But there are more important differences between *Lodevopterum* and *Euremisca* Zalessky, 1951, viz. the base of RP is at the same point as the point of separation of MA from MP in *Euremisca* while well distad this point in *Lodevopterum*; no stem of M well separated from R in *Euremisca*, vs a long stem well separated from R in *Lodevopterum*. Indeed, as there is no clear synapomorphy of the Euremiscidae, the proposal of Aristov is only tentative. Unfortunately, there are many other cases of this kind in the current classification of the 'Grylloblattodea'. Consequently, as for *Lodevopterum*, it is not possible to accurately – using apomorphy or synapomorphy – attribute the new fossil to a precise family.

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Conflict of interest statement

No conflict of interest.

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