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The insect fauna from the Permian of Lodève (Hérault, France): state of the art and perspectives

La fauna de insectos del Pérmico de Lodève (Hërault, Francia): estado de los conocimentos y perspectivas

O. Béthoux

Dresden Museum of Zoology, Königsbrücker Landstraße 159, D-01109 Dresden, Germany
obethoux@yahoo.fr

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Abstract

An up-to-date list of non-blattoid insect taxa from the Late Permian Salagou Formation is provided. The taxonomic and phylogenetic importance of these taxa is stressed. A research program is proposed that would allow the biostratigraphic and ecological significance of this fauna to be better appreciated.

Keywords: Insect, Permian, taxonomy, phylogeny, palaeoecology, assemblage.

Resumen

Se proporciona una lista actualizada de los taxones de insectos no blatoideos de la Formación Salagou (Pérmico Superior). Se resalta la importancia taxonómica y filogenética de estos taxones. Se propone un programa de investigación enfocado hacia una mayor incidencia de la importancia biostratigráfica y ecológica de esta fauna.

Palabras clave: Insecto, Pérmico, taxonomía, filogenia, paleoecología, asociación.

1. Introduction

The description of the Permian insect fauna from the Lodève basin (Salagou Formation) is an ongoing project, with the first taxonomic publication dating back to 1999. The collection resulted from tirelessness and scrutiny of Dr. J. Lapeyrie and his family, who investigated the Salagou Formation for years. Their effort resulted into a collection of several hundreds of specimens, ranging from the smallest fragments to large-sized wings of dragonflies. Later researchers made some additions to the collection, which is currently housed at the Muséum National d'Histoire Naturelle of Paris for study.

2. Taxonomic results

To date, representatives of eight major groups of insects have been described. Among them the Odonatoptera (dragonflies, damselflies) are represented by four species, the †Diaphanopterodea by three species, and the †Pal-

aeodictyoptera by a single species. Among neopterous insects, the †Glosselytrodea (an extinct holometablous order; one species), the Orthoptera (grasshoppers, crickets; three species), the †Caloneurodea (an extinct order related to Orthoptera; two species), the '†Strephocladida' (a group of polyneopterous insects of uncertain affinities; one species), and the '†Grylloblattida' (a group of polyneopterous insects of uncertain affinities; two species) are represented (Fig. 1). This makes a total of 17 described species. However, members of the orders Blattaria (cockroaches), †Protelytroptera, Hemiptera (bugs), and Neuroptera are to be described, and several representatives of the Odonatoptera and Orthoptera are yet undescribed.

From a taxonomic point of view, the early steps of this project already yielded important results, with nine of the 17 described species belonging to new genera (see annex 1). Additionally, new information on previously known taxa was obtained from this record, such as the range of forewing venation variability in the Orthoptera species *Iasvia reticulata* Zalessky, 1934 (Fig. 1A; Béthoux *et al.*, 2002b; hind wing morphology of this taxon remains to be described after the Lodève abundant material).

Discovery and identification of *Raphogla rubra* Béthoux *et al.*, 2002a (Fig. 1B) and of *Permostridulus brongniarti* Béthoux *et al.*, 2003b are particularly significant. The former species is the sister group of the whole suborder Ensifera (crickets; Béthoux *et al.*, 2002a). It provided valuable clues regarding the plesiomorphic state of wing venation in the group, allowing the major inner clades of Ensifera to be redefined (Béthoux and Nel, 2002). In the case of *P. brongniarti*, this species happened to be the earliest stridulating representative of a clade including the Orthoptera plus several other orders. As far as I am aware, this constitutes the earliest evidence of sound producing device in animal kingdom (Béthoux *et al.*, 2003b). Moreover, this discovery, implemented by the identification of new material from Elmo, allowed a new hypothesis on the wing venation of the order Caloneurodea to be proposed (Béthoux *et al.*, 2004).

Decade- or century-old issues of insect wing venation nomenclature, themselves resulting into contradictory phylogenetic hypotheses, impeded descriptions and identifications of the Lodève insect taxa. For example, the study of the Orthoptera material faced the problem of several contradictory wing venation interpretations, available in literature data, a situation linked to the 'Protorthoptera waste-basket group' problem. This issue prompted a review of Palaeozoic representatives of the group, resulting into the definition of a clade of superordinal relevance, namely the Archaeorthoptera Béthoux and Nel, 2002. Subsequent works dedicated to Carboniferous and Permian taxa (Béthoux, 2003; Béthoux and Nel, 2003, 2005a,b; among others) led to new hypotheses regarding early insect evolution (Béthoux, 2005a). Clearly, there is a trade-off between clues provided by the Lodève fauna and simultaneous review of material from other Palaeozoic and Triassic deposits. This is because the taxonomy and phylogeny of Palaeozoic insects is yet a matter of strong debate [compare, for example, insect phylogenies as provided in Kukalová-Peck (1991), Rasnitsyn and Quicke (2002), and Grimaldi and Engel, (2005)]. Thereafter new material is likely to provide significant new information, as exemplified above. This fact renders further study of Lodève material essential.

3. Perspectives

The fact that nearly half of described species belong to new genera and higher rank taxa suggests that the Lodève assemblage represents a fauna of particular ecological preferences, and/or that the Permian insect fauna as a whole is poorly known. However, the latter view must be balanced because differences / similarities between Palaeozoic fossil insect assemblages could be significant at a supra-generic level, as suggested by Béthoux [in press; see also a comparison of several Permian assemblages of grylloblattid insects by Storozhenko (1998) at the familial level].

In order to test this hypothesis, data on species abundance from contemporaneous deposits are sorely needed. First, this would allow the quality of our knowledge of Permian insect faunas to be assessed. Obtaining species rarefaction curves (Colwell and Coddington, 1994; Gotelli and Colwell, 2001) might allow one to infer the total species richness of the fossil assemblage by using a set of estimators, for example those in use in EstimateS software (Colwell, 2004). In turn the collecting effort (significance of the available material regarding the whole fossil assemblage) would be measured using the completeness ratio *C* of Soberón *et al.* (2000) [which is, basically the ratio (collected species / predicted species), and is then readily applicable to fossil faunas]. Additionally, this measurement would allow a better appreciation of collecting priorities among different outcrops.

Thereafter, based on deposits that are adequately sampled, orders could be ranked according to their dominance, in terms of species richness and individuals. Assuming that corrective ratios could be obtained from taphonomic studies based on the content of modern sediments [with respect to surrounding living assemblages (see the isolated work of quantitative experimental taphonomy of insects by Smith (2000)], one would eventually rigorously

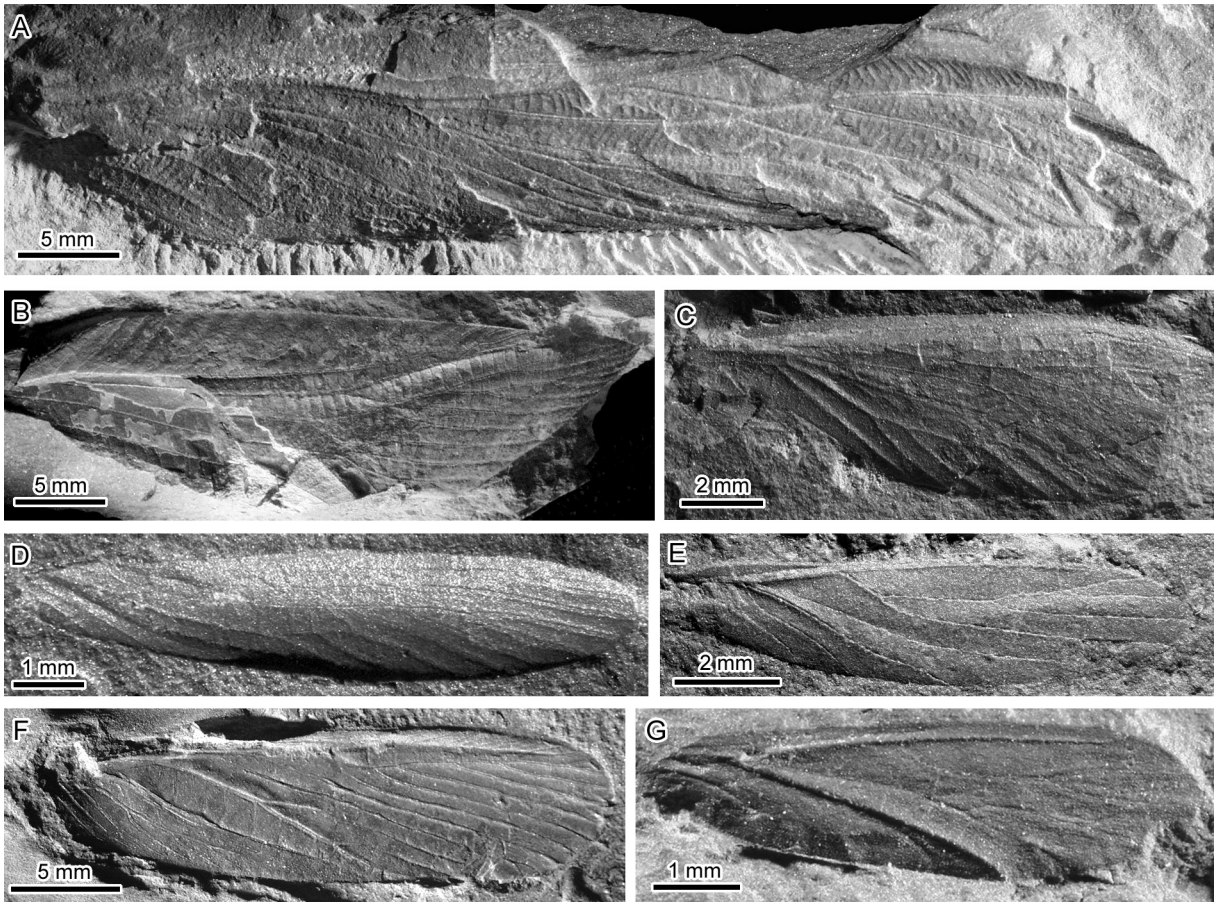

Fig. 1.- Examples of insect taxa described from the Permian of Lodève; all specimens belong to the Lapeyrie collection. **A.** *Iasvia reticulata* Zalessky, 1934 (Orthoptera; specimen Ld LAP 576, right forewing, positive imprint). **B.** *Raphogla rubra* Béthoux *et al.*, 2002a (Orthoptera; specimen Ld LAP 415, right forewing, negative imprint, reversed). **C.** *Depressopterum minutus* Béthoux *et al.*, 2005 (Grylloblattida; specimen Ld LAP 136, left forewing, positive imprint, reversed). **D.** *Lodevopterum angustus* Béthoux *et al.*, 2005 (Grylloblattida; specimen Ld LAP 132, right forewing, negative imprint, reversed, light-mirrored). **E.** *Phaneroneura minuta* Béthoux *et al.*, 2003c (Diaphanopterodea; specimen Ld LAP 305, right wing, positive imprint). **F.** *Tococladus garrici* Béthoux *et al.*, 2003a ('Strephocladida'; specimen Ld LAP 308, right forewing, positive imprint). **G.** *Nanogramma gandi* Béthoux *et al.*, 2004 (Caloneurodea; specimen Ld LAP 369, right wing, positive imprint).

Fig. 1.- Ejemplos de taxones de insectos descritos en el Pérmico de Lòdeve. Todos los especímenes pertenecen a la colección *Lapeyrie*. **A.** *Iasvia reticulata* Zalessky, 1934 (Orthoptera; specimen Ld LAP 576, right forewing, positive imprint). **B.** *Raphogla rubra* Béthoux *et al.*, 2002a (Orthoptera; specimen Ld LAP 415, ala externa derecha con impresión negetiva). **C.** *Depressopterum minutus* Béthoux *et al.*, 2005 (Grylloblattida; specimen Ld LAP 136, ala izquierda externa con impresión positiva). **D.** *Lodevopterum angustus* Béthoux *et al.*, 2005 (Grylloblattida; specimen Ld LAP 132, ala externa derecha con impresión negatica y luz reflejada). **D.** *Lodevopterum angustus* Béthoux *et al.*, 2005 (Grylloblattida; specimen Ld LAP 132, ala derecha con impresión positiva). **F.** *Tococladus garrici* Béthoux *et al.*, 2003a ('Strephocladida'; specimen Ld LAP 308, ala externa derecha con impresión positiva). **G.** *Nanogramma gandi* Béthoux *et al.*, 2004 (Caloneurodea; specimen Ld LAP 369, ala derecha con impresión positiva).

compare Permian faunas, and possibly decipher local characteristics from global trends.

Another impact of the distinctiveness of the Lodève fauna, as currently known, is that biostratigraphical inferences based upon non-blattoid insects are premature. Indeed the research program drawn above would allow one to tease apart temporal from ecological characteristics of assemblage composition, at any relevant taxonomic level, by comparing contemporaneous deposits of various ecological settings.

However, there is no doubt that facilities currently involved in the study of Palaeozoic fossil insects, despite the overall domination of the class in modern continental ecosystems (in terms of diversity, disparity, and ecological importance), are insufficient for completing such a research program..

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Annex 1: Described taxa from the Salagou Formation

Odonatoptera

Saxonagrion Nel *et al.*, 1999a
Saxonagrion minutus Nel *et al.*, 1999a
Lapeyria Nel *et al.*, 1999b
Lapeyria magnifica Nel *et al.*, 1999b
Lodevia Nel *et al.*, 1999c
Lodevia longialata Nel *et al.*, 1999c
Epilestes Martynov, 1937
Epilestes gallica Nel *et al.*, 1999c

Palaeodictyoptera

Lodetiella Béthoux *et al.*, 2007
Lodetiella magnifica Béthoux *et al.*, 2007

Diaphanopterodea

Phaneroneura Carpenter, 1947
Phaneroneura minuta Béthoux *et al.*, 2003c (Fig. 1E)
Salagouneura Béthoux *et al.*, 2003c
Salagouneura chimaira Béthoux *et al.*, 2003c
Martynovia Tillyard, 1932
Martynovia aff. *insignis* Tillyard, 1932
Martynovia sp.

Glosselytrodea

Surijoka Martynova, 1958
Surijoka lutevensis Béthoux *et al.*, 2001

Orthoptera

Raphogla Béthoux *et al.*, 2002a
Raphogla rubra Béthoux *et al.*, 2002a (Fig. 1B)
Iasvia Zalessky, 1934
Iasvia reticulata Zalessky, 1934 (Fig. 1A)
Iasvia secunda Béthoux *et al.*, 2002b

Caloneurodea

Permostridulus Béthoux *et al.*, 2003b
Permostridulus brongniarti Béthoux *et al.*, 2003b
Nanogramma Béthoux *et al.*, 2004
Nanogramma gandi Béthoux *et al.*, 2004 (Fig. 1G)

'Strephocladida'

Tococladus Carpenter, 1966
Tococladus garrici Béthoux *et al.*, 2003a (Fig. 1F)

'Grylloblattida'

Lodevopterum Béthoux *et al.*, 2005
Lodevopterum angustus Béthoux *et al.*, 2005 (Fig. 1D)
Depressopterum Kukalová, 1964
Depressopterum minutus Béthoux *et al.*, 2005 (Fig. 1C)