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A new middle Permian orthopteran family questions the position of the Order Titanoptera (Archaeorthoptera: Orthoptera)

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Legendreia magnifica gen. et sp. nov., the type species of the new family Legendreiidae fam. nov., is described from the middle Permian Yinping Formation of China, on the basis of a complete forewing. Its unique pattern of venation of the cubital area allows us to question a previous hypothesis of a phylogenetic relationship between the orthopteran family Tcholmanvissiidae and the 'order' Titanoptera. If the latter clearly belongs to the clade Panorthoptera, its current position in Orthoptera is weakly supported and will need further investigation.

http://zoobank.org/urn:lsid:zoobank.org:pub:B735828F-05A8-43A8-ACCC-B4908B03E3A2

Keywords: Insecta; Panorthoptera; phylogeny; venation; Paleozoic

Introduction

The very large superorder Archaeorthoptera (or 'orthopteroid' insects) flourished during the late Carboniferous and Permian, with high familial, generic and species-level diversities and an important disparity of structures. Unfortunately, many of their fossils consist only of more-or-less complete wings and, generally, tegmina. The venation in this clade shows a series of synapomorphies, as defined by Béthoux & Nel (2002a), which allow accurate placement of fossils in this clade. Archaeorthoptera is composed of a stem group plus the orders Caloneurodea Martynov, 1938, Cnemidolestodea Handlirsch, 1937, Titanoptera Sharov, 1968, and Orthoptera Olivier, 1789. The relationships between these 'orders' and even, in some cases, their monophyly, remain debatable. This is especially the case for the relatively small late Paleozoic–Triassic group Titanoptera, which is placed currently in Orthoptera but was previously considered as Panorthoptera (the stem group of the Orthoptera *sensu stricto*) (Béthoux & Nel 2002b; Béthoux 2005, 2007). Its current position in Orthoptera is based on an alleged 'grade' between the Permian orthopteran family Tcholmanvissiidae and the Titanoptera *sensu stricto* (Béthoux 2007) and is supported by a particular pattern of the forewing cubital veins.

Here, we describe a new Chinese middle Permian orthopteran, based on a very well-preserved complete forewing that allows us to consider the homology of venation in Tcholmanvissiidae and Titanoptera, which leads us to question the affinities of the latter 'order'.

Material and methods

The specimen was collected from the middle section of the middle Permian Yinping Formation (Capitanian stage of the Guadalupian epoch) of Anhui Province, China. The fossil-bearing layer is a black shale representing a marine-terrestrial interfacies deposit that has produced various species (e.g. Huang *et al*. 2007; Lin *et al*. 2010; Ponomarenko *et al*. 2014; Swedo & Huang 2019).

The wing was prepared using a sharp knife. Photographs were taken using a digital camera attached to a Zeiss Discovery V16 microscope. The holotype is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

We follow the wing venation terminology of Béthoux & Nel (2002a), as confirmed by the recent work of Desutter-Grandcolas *et al*. (2017), on the basis of a careful study of the origins of the main veins in the wing base and their distal fusions and subdivisions, adapted for the Tcholmanvissiidae by Béthoux (2007), with an emendation for the vein AA1 *sensu* Béthoux & Nel (2002a, 2003), which is in fact the PCu, as shown in Schubnel *et al*. (2019). We reject the old hypothesis

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of Sharov (1968) and the 'Russian' school for the pattern of wing venation of the Polyneoptera (Aristov 2017), which was based only on the relative positions of the main veins, while neglecting other evidence (relative convexity of the veins and the courses of the veins from the basivenal bullae situated in the extreme wing base, which are visible only with X-ray tomography: see Jacquelin *et al*. 2018; Schubnel *et al*. 2019).

Anatomical abbreviations

A: anal veins; **CuA:** cubitus anterior, **CuP:** cubitus posterior; **CuPa:** anterior branch of CuP; **CuPaα:** anterior branch of CuPa; **CuPaα°:** most anterior branch of CuPaα ending in CuA; **CuPaα*:** posterior branch of CuPaα; **CuPaβ:** posterior branch of CuPa; **CuPb:** posterior branch of CuP; **M:** median vein; **MA:** median anterior, **MP:** median posterior; **PCu:** post-cubital vein; **R:** radius; **RA:** radius anterior; **RP:** radius posterior; **ScA:** subcostal anterior; **ScP:** subcostal posterior.

Systematic palaeontology

Class **Insecta** Linnaeus, 1758
Superorder **Archaeorthoptera** Béthoux and Nel, 2002a
Panorthoptera Crampton, 1928
Order **Orthoptera** Olivier, 1789
Family **Legendreiidae** fam. nov.

Included taxa. Only the type genus *Legendreia* gen. nov.

Type species. *Legendreia magnifica* sp. nov.

Diagnosis. Forewing characters only. Basal part of precostal area very broad; MA not approximating RP; a regular net of rectangular cells in all wings; a free basal branch CuPaα* of CuPaα not ending in CuA; CuPaβ in a very basal position; CuPb distally forked; PCu simple; anal veins simple.

Genus ***Legendreia*** gen. nov.

Type species. *Legendreia magnifica* sp. nov.

Etymology. Named after our friend and colleague Frédéric Legendre, a specialist on Dictyoptera. Gender feminine.

Diagnosis. RA anteriorly pectinate with long branches; RP, MA, and CuA posteriorly pectinate; MP simple.

Legendreia magnifica sp. nov.
(Figs 1, 2)

Diagnosis. As for the genus, forewing very large.

Etymology. Named after the wonderful state of preservation of the type specimen.

Holotype. NIGP 171019, imprint of complete forewing and counter-imprint of wing base.

Description. Imprint and counter-imprint of a complete and well-preserved forewing with a series of spots apparently organized in transverse bands on the distal half of wing (which might represent remnants of the original coloration); wing elongate, 45.0 mm long; 12.0 mm wide; a 'precostal' area, broad with an anterior 'lobe', a fan of veinlets and a net of small cells, posteriorly limited by a simple convex vein ScA that goes into costal margin 11.6 mm from wing base; concave ScP appressed to R at wing base, area between anterior wing margin and ScP broad, 2.1 mm wide; anterior branches of ScP simple; 2–3 crossveins between them; ScP distally approximating RA but never touching it, reaching anterior wing margin 10mm from wing apex; MP + CuA separated from R near wing base, appressed to it for 2.1 mm, and distinctly separated from R distally; distal independent stem of MP + CuA 3.7 mm long; presence of short crossveins between R and stem M + CuA; R forked into a convex RA and a concave RP 16.7mm from wing base; RA anteriorly pectinate with five branches; RP posteriorly pectinated with six branches; M and CuA separated 9.3 mm distal of wing base; M divided into MA and MP 1.1 mm distally; MA with three posterior branches, never approximating RP; MP simple; free part of CuA short, 2.1 mm long; CuPaα° very short ending in CuA, CuA + CuPaα° posteriorly pectinate with eight branches; CuP divided into CuPa and CuPb 3.4 mm from wing base; CuPa very short, 1.0 mm long before its subdivision into CuPaα and CuPaβ; CuPaα with an independent branch CuPaα* not ending in CuA; CuPaβ simple very close to separation between CuPa and CuPb (Fig. 2); CuPb distally divided into two branches; a simple PCu vein clearly emerging from a strongly curved bulla at wing base; two simple 'anal' veins, with large transverse cells between them; crossveins generally regular and cells rectangular.

Occurrence. The late middle Permian Yinping Formation; near Houdong Village, Chaohu District, Hefei City, Anhui Province, China.

Discussion

The pattern of wing venation in *Legendreia* gen. nov. corresponds exactly to that of the clade Archaeorthoptera Béthoux & Nel, 2002a, as verified by

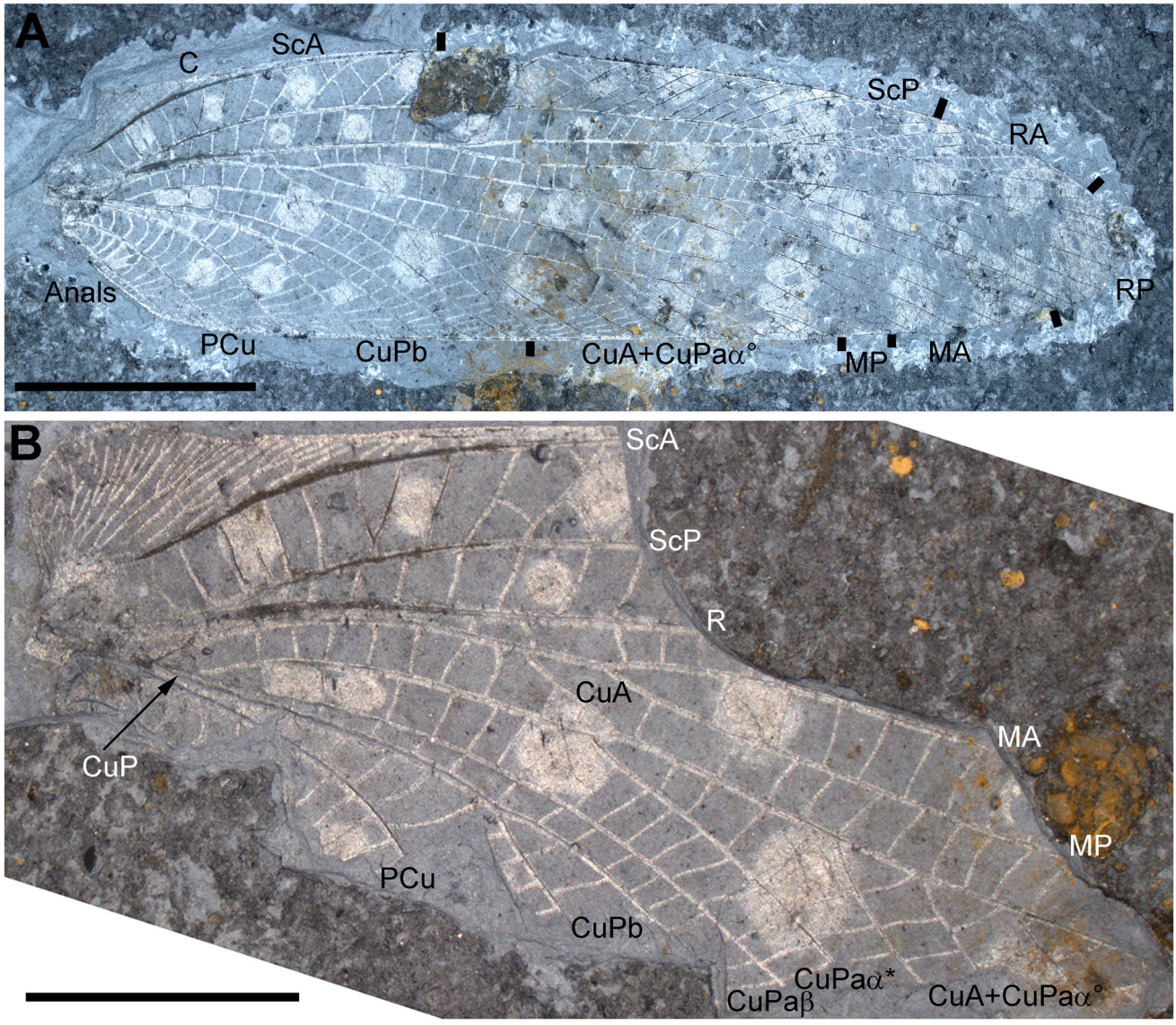

Figure 1. *Legendreia magnifica* gen. et sp. nov., holotype NIGP 171019. **A,** imprint of tegmen; **B,** counter-imprint (photograph in mirror). **Abbreviations: A**, anal veins; **CuA,** cubitus anterior; **CuP,** cubitus posterior; **CuPa,** anterior branch of CuP; **CuPaα**, anterior branch of CuPa; **CuPaα°**, most anterior branch of CuPaα ending into CuA; **CuPaα***, posterior branch of CuPaα; **CuPaß**, posterior branch of CuPa; **CuPß**, posterior branch of CuP; **M,** median vein; **MA,** median anterior; **MP,** median posterior; **PCu,** post-cubital vein; **R,** radius; **RA,** radius anterior; **RP,** radius posterior; **ScA,** subcostal anterior; **ScP,** subcostal posterior. Scale bars = 10 mm (A); 5 mm (B).

Desutter-Grandcolas *et al*. (2017) on the basis of extant Ensifera: basal fusion of M with CuA, both appressed to R, a distal re-emergence of a convex M + CuA, a separation of M + CuA into a M and a CuA, a concave CuP that divides into CuPa and CuPb, and CuPa ending into CuA. *Legendreia* gen. nov. has the main synapomorphy of Panorthoptera, *viz*. a concave posterior branch CuPaβ of CuPa separating basal to fusion of the other branch CuPaα of CuPa with CuA.

A more curious character of *Legendreia* gen. nov. is the distally forked CuPb. A CuPb with distal forks is also present in the panorthopteran Geraridae Scudder, 1885 and the Archaeorthoptera *nec*. Panorthoptera Stenoneuridae Brongniart, 1894 (*sensu* Béthoux & Nel 2002a). Note that this character can vary in Geraridae (see Béthoux & Nel 2003). However, in Geraridae, there are more veinlets forming a net of irregular cells between the branches of CuPb, while those of *Legendreia* gen. nov. are simple. In Orthoptera (*sensu* Béthoux and Nel 2002a), the CuPb is simple. Members of Geraridae differ from *Legendreia* gen. nov. in the presence of a ramified PCu (AA1 *sensu* Béthoux & Nel

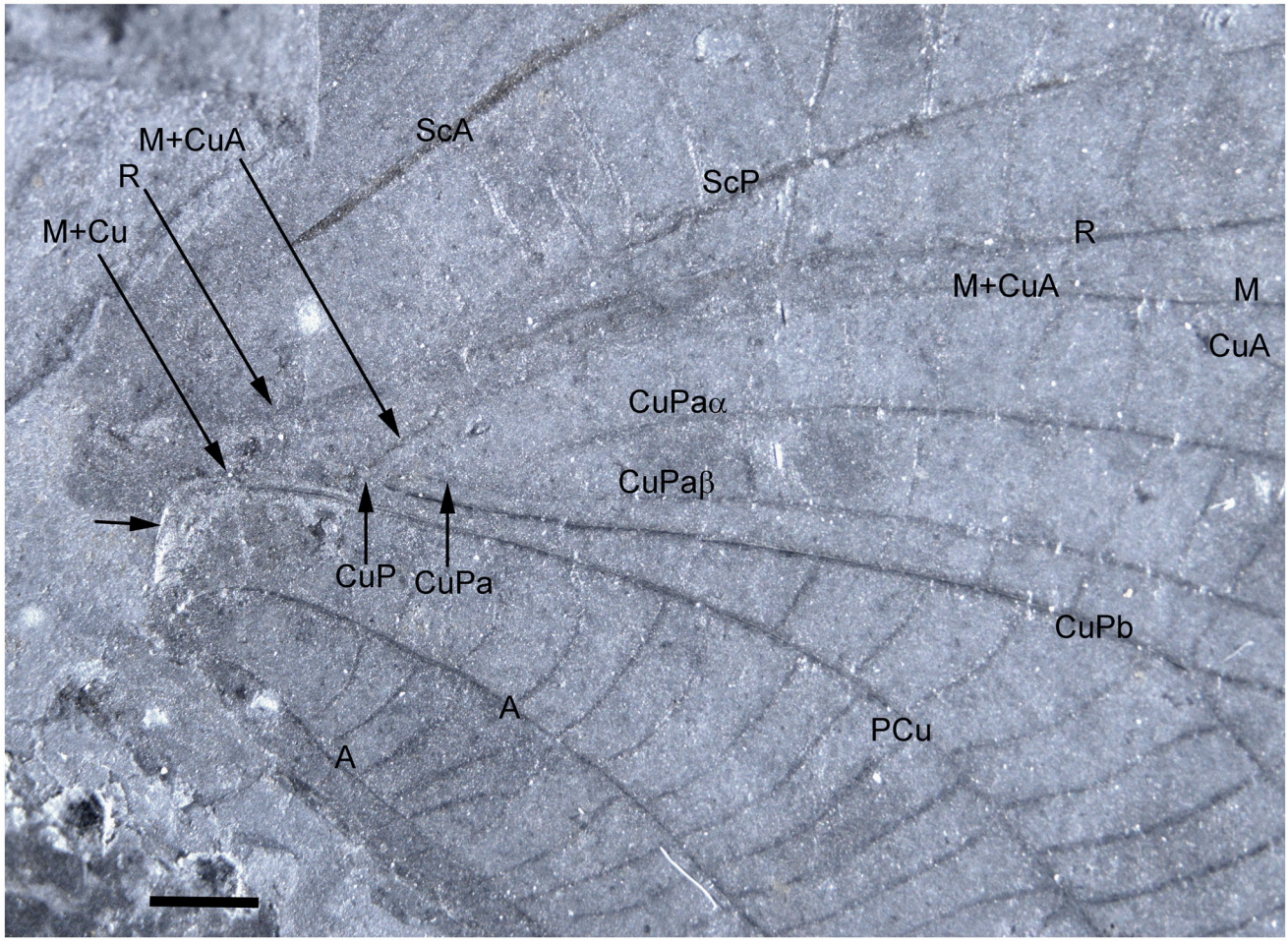

Figure 2. *Legendreia magnifica* gen. et sp. nov., holotype NIGP171019. Base of tegmen, arrow bulla of PCu. **Abbreviations: A,** anal veins; **CuA,** cubitus anterior; **CuP,** cubitus posterior; **CuPa,** anterior branch of CuP; **CuPaα,** anterior branch of CuPa; **CuPaα°**, most anterior branch of CuPaα ending into CuA; **CuPaα***, posterior branch of CuPaα; **CuPaß,** posterior branch of CuPa; **CuPß,** posterior branch of CuP; **M,** median vein; **MA,** median anterior; **MP,** median posterior; **PCu,** post-cubital vein; **R,** radius; **RA,** radius anterior; **RP,** radius posterior; **ScA,** subcostal anterior; **ScP,** subcostal posterior. Scale bars = 1 mm.

2002a, 2003), in forked anal veins, in the presence of a MA strongly approximating RP, cells in the basal half of the wing are irregular rather than being rectangular, and in a narrower precostal area.

A second important character of *Legendreia* gen. nov. is the presence of a free basal branch CuPaα* of CuPaα not ending in CuA as in the Tcholmanvissiidae Zalessky, 1934 (as revised in Béthoux & Nel 2002b). But in Tcholmanvissiidae, although CuPaα* is in a very distal position, as in *Legendreia* gen. nov., the vein CuPaβ is not in the very basal position seen in *Legendreia* gen. nov.

Legendreia gen. nov. has a M + CuA well-separated from R at the extreme wing base. A similar situation occurs in the late Carboniferous panorthopteran *Bruaylogus magnificus* Coty *et al*., 2014 in which M + CuA is appressed to R only for a short distance and is not fused to it (Coty *et al*. 2014). Even in Tcholmanvissiidae, the two veins R and M + CuA are very close but not appressed. *Legendreia* gen. nov. shares with these taxa the presence of a series of very short crossveins between these veins (Béthoux & Nel 2002b).

More recently, Béthoux (2007, p. 138) indicated: "As do other tcholmanvissiidaeans, *beybienkoi* and *gigantea* exhibit one or several posterior branches of CuPaα occurring basal to the connection with CuA (Béthoux & Nel 2002b). This is a strict apomorphic character state within Neoptera." This putative synapomorphy would suggest a relationship between *Legendreia* gen. nov. and Tcholmanvissiidae, but it is also present in *Uraloedischia* Sharov, 1968, which is currently placed in Oedischiidae Handlirsch, 1906 (Gorochov 1995, fig. 133). This last genus could belong to Tcholmanvissiidae also, but needs to be revised. Gorochov (1995) considered the Tcholmanvissiidae to be a subfamily of

Oedischiidae, thus the current classification of these insects is rather confusing.

Béthoux (2007, fig. 3) considered Tcholmanvissiidae to be a paraphyletic set of taxa from which the 'orthopteroid' Titanoptera emerged. This author proposed the following evolutionary sequence between the Panorthoptera, Tcholmanvissiidae and Titanoptera – presence of CuPaα, CuPaβ and CuPb → presence of a CuPaα* → partial fusion of CuPaα* with CuPaβ → fusion of CuPaβ (+ posterior branch of CuPaα*) with CuPb – to explain the forked CuPb in Titanoptera. He considered that in the tcholmanvissiid *Jubilaeus beybienkoi* Sharov, 1968 and *Tcholmanvissiella gigantea* Gorochov, 1987, there is partial fusion of CuPaα* with CuPaβ and that in the titanopteran *Mesotitan giganteus* Tillyard, 1916 and *Gigatitan extensus* (Sharov, 1968) this vein is basally fused to CuPb and re-emerges distally (see Béthoux 2007, fig. 1). Evidence for this hypothesis is not obvious because all of these veins are concave. Furthermore, the discovery of *Legendreia* gen. nov. shows that CuPb can be distally forked without any involvement of the vein CuPaβ in this phenomenon because CuPaβ is completely independent of CuPb in this taxon. Thus, even if the hypothesis of a fusion of CuPb with CuPaβ (plus a posterior branch of CuPaα*) in Titanoptera as proposed by Béthoux (2007) remains possible, it is not absolutely demonstrated, and is in part contradicted by the condition in *Legendreia* gen. nov. If one considers that the CuPb in Titanoptera is distally branched without any basal fusion with CuPaβ, then the 'CuPaα*' (*sensu* Béthoux 2007) of Titanoptera becomes CuPaβ and CuPaα has no basal branch CuPaα*, it renders obsolete the hypothesis of a relationship between Titanoptera and Tcholmanvissiidae. Béthoux (2005, p. 405) supposed that Titanoptera was the sister group of Geraridae on the basis of "the following two characters that are probably apomorphic: in forewings, vein CuPaβ branched; in hind-wings, vein CuPb branched."

The presence of a forked CuPb in some Archaeorthoptera, Panorthoptera and Titanoptera questions the polarity of this character state. In the most recent and comprehensive phylogeny of Polyneoptera (Wipfler *et al*. 2019), the Orthoptera are considered as the sister group of the clade (((Mantophasmatodea + Grylloblattodea) + (Embioptera + Phasmatodea)) + Dictyoptera). All the winged representatives of these orders, and Paoliida, currently considered as the fossil sister group of the Dictyoptera (Prokop *et al*., 2014), have a simple CuP. Plecoptera, the sister group to the set of all these clades, also have a simple CuP. Thus, it is likely that the forked CuPb of some archaeorthopterans is a derived character state. Nevertheless, it is probably subject to convergence, at least between the Stenoneuridae, Geraridae and Tcholmanvissiidae, because these taxa strongly differ in too many other wing venation characters to be closely related.

Nevertheless, *Legendreia* gen. nov. shares with Tcholmanvissiidae an important set of characters: precostal area very large and rounded; a long ScA; ScP distally approximating RA but not fused with it; RA with long anterior branches; a broad area between RA and RP; MA with numerous branches while MP is simple; MA and RP not approximating; nearly all cells rectangular with those of the cubito-anal areas transverse, limited by more or less curved crossveins; and presence of a CuPaα* (putative synapomorphy). *Legendreia* gen. nov. differs from all tcholmanvissiids in the forked CuPb and the base of the CuPaβ being very close to the fork of CuP.

Conclusions

The discovery of *Legendreia* gen. nov. confirms that the Permian diversity of 'orthopteroid' insects was very high. It also shows that the phylogenetic relationships between these insects remain weakly supported. If Titanoptera, recorded in the Permian and Triassic, belongs to Panorthoptera, the hypotheses of relationships between them and Tcholmanvissiidae are weakly supported, based on putative fusions of some branches of the cubitus posterior that would explain the presence of a forked CuPb. The pattern of venation of *Legendreia* gen. nov., which lacks such fusions and has a forked CuPb, shows that this hypothesis will need further investigation to be confirmed. Unfortunately, the majority of these Permian insects are imperfectly known on the basis of isolated wings only. Future field research and discoveries of more complete specimens will be necessary to clarify this situation.

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