A Triassic palaeodictyopteran from Kyrgyzstan

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Abstract

A specimen belonging to the species *reliquia* n. sp. is described from the Dzaylyaucho locality (Madygen, Kyrgyzstan; late Middle to early Late Triassic). It is interpreted as a palaeodictyopteran. It is therefore the latest occurrence of this group, previously considered as extinct during Middle to earliest Late Permian.

Keywords: Madygen, Insecta, Palaeodictyoptera, *reliquia* n. sp., *Liquia reliquia* n. gen. et sp., relic species.

Zusammenfassung

Beschrieben wird ein Insektenflügel der Art *reliquia* n. sp. von der Fundstelle Dzaylyaucho (Madygen, Kirgisistan; späte Mittel- bis frühe Obertrias). Er wird als Palaeodictyoptere interpretiert. Es handelt sich damit um den stratigraphisch jüngsten Nachweis dieser Gruppe, von der bislang angenommen wurde, dass sie im Mittleren bis frühen Späten Perm ausgestorben ist.

1. Introduction

New collects at the famous Triassic Dzaylyaucho locality (Madygen, Kyrgyzstan; late Middle to early Late Triassic) were carried out during summer 2007, with the prospect of improving our knowledge of the entomofauna documented from this locality. Collected material is mainly composed of blattodeans, homopterans, and orthopterans, in addition to a number of rarer groups. The taxonomy of the amassed material is currently investigated. Herein we describe a fossil specimen that cannot be assigned to any of the groups listed by Shcherbakov (2008) from this locality. It turns out to be the latest representative of a group supposedly extinct at the end of the Permian.

Abbreviations, preparation, and convention

The wing venation nomenclature follows the serial insect wing venation pattern paradigm (Lameere 1922, 1923). Wing venation abbreviations relevant for this contribution are repeated for convenience: ScP, posterior Subcosta; R: Radius; RA: anterior Radius; RP, posterior Radius; M, Media; MA, anterior Media; MP, posterior Media; CuA, anterior Cubitus; CuP, posterior Cubitus; AA, anterior Analis. In order to prevent the formation of gypsum crystals on the surface of the specimen, it was covered with Polyvinylacetat (PVAc) when collected. This cover can be removed with ethanol. Vein concavity and convexity are described as if viewed from dorsal side (and positive imprint).

Acronym of depository

FG	Technical University Bergakademie Freiberg, Institute of Geology, Department of Palaeontology

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2. Systematic palaeontology

The cladotypic nomenclatural procedure (see Béthoux 2007a, 2007b, 2007c, 2010) is followed herein. We refer the readers to an introduction to the procedure provided in Béthoux & Herd (2009). If a taxon is undefined under cladotypic taxonomy it will be referred to by a vernacular version of its Linnaean traditional name (i. e. palaeodictyopteroideans are members of the Linnaean super-order Palaeodictyopteroidea), to avoid mixing cladotypic and Linnaean taxon names. A formal Linnaean genus name is erected in Appendix in order to allow the mention of the new species under a traditional nomenclatural framework.

Species *reliquia* n. sp.
Fig. 1

Holotypus: Specimens FG 596/IV/120a (negative imprint) and FG 596/IV/120b (positive imprint).

Derivatio nominis: After ‘relic’ in Latin.

Stratum typicum: “Upper Grey-coloured Member” (T4), Madygen Formation (Ladinian/Carnian, late Middle to early Late Triassic, according to Dobruskina 1995).

Locus typicus: Sharov quarry (No. 14; Dobruskina 1995), northwestern Madygen outcrop area (Urochishche Dzaylyaucho), Batken district (Oblast), southwest Kyrgyzstan.

Diagnosis. – RA, MA, and CuA simple; branches of MP fused with CuA and diverging anteriorly from it; five transversal dark stripes.

Description. – Positive and negative (Fig. 1b) imprints of a right wing, disrupted in three parts (referred to as basal, median, and apical fragments), apex missing; preserved length about 31 mm, estimated length about 31.5 mm, estimated width about 14.3 mm; anterior wing margin with a bump near the wing base; ScP concave,

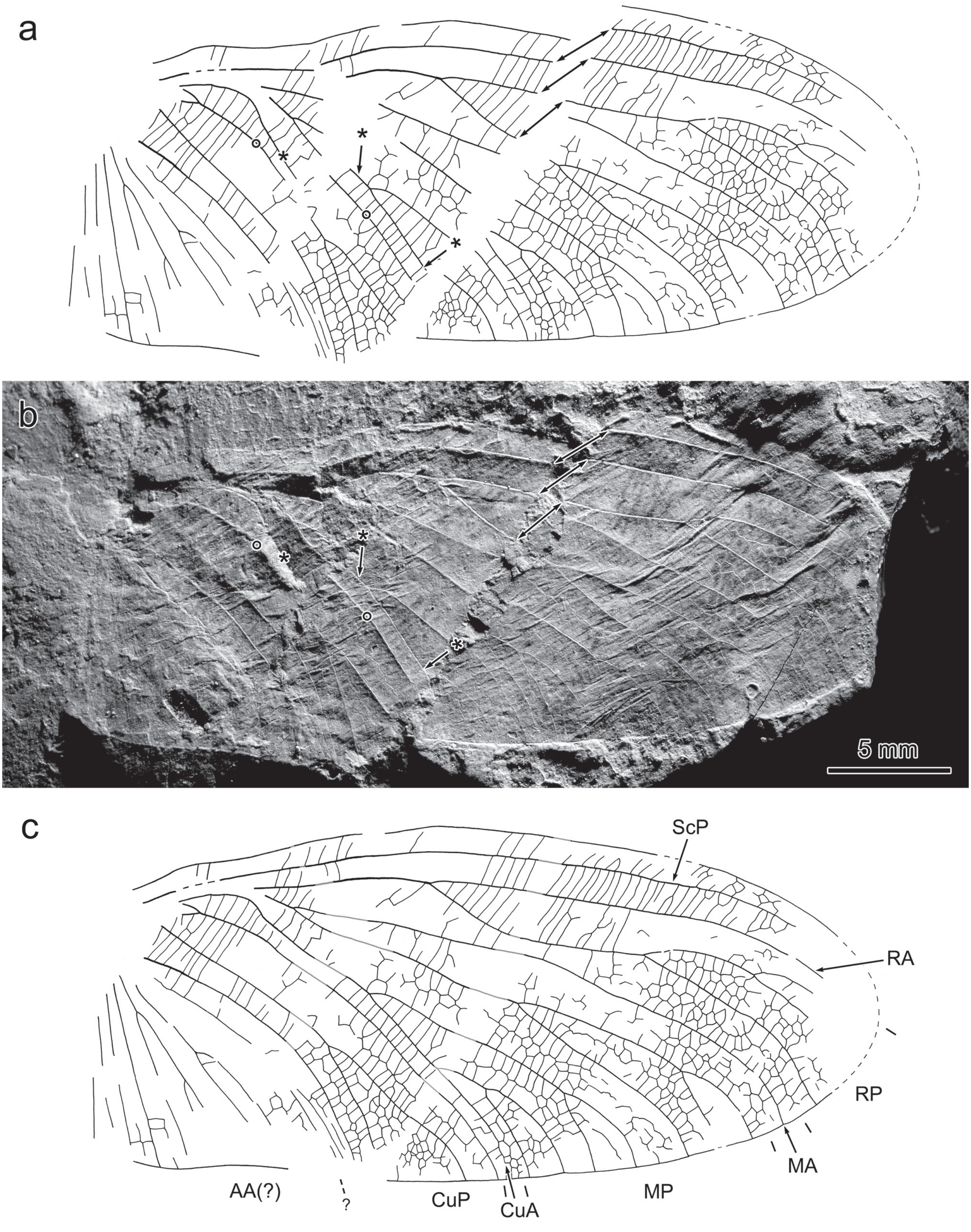

Fig. 1. Species *reliquia* n. sp., holotype, FG 596/IV/120. – **a**. Drawing of the wing venation. **b**. Photograph of the negative imprint, reversed. **c**. Restoration of the wing.

simple, reaching wing apex; R and RA convex, reaching wing apex; RA and RP diverge near wing mid-length; RA simple; RP concave, branched distal to its mid-length, with three terminal branches (as preserved); M and its branches concave; MA simple, MP (distinct from CuA?) with three terminal branches; (stem of?) CuA convex, with concave branches (belonging to MP?) diverging anteriorly, totalizing four terminal branches in addition to the posterior stem; near wing base, strut (?) occurring between CuA and the vein immediately posterior to it; area between (the posterior stem of) CuA (* on Fig. 1a, b) and (the first?) CuP vein (° on Fig. 1a, b) narrow; area posterior to (the first?) CuP vein and the next vein broad; posterior to (the first?) CuP vein occur two concave veins, forked and simple, respectively; posterior to these veins occur several convex vein arranged in fan; along the posterior wing margin, in the apical area, and in all broad inter-veinal areas, crossveins reticulated, with two to four rows of cells; five transversal oblique dark stripes (one located along the right edge of the basal fragment, another along the right edge of the median fragment, three in the distal fragment).

Discussion. – For simplicity, the description follows the reconstruction and the wing venation interpretation discussed thereafter. Establishing correspondence between the median and apical fragments poses no major issues. Correspondence between the basal and median parts was established based on several landmarks. Posterior to ScP, which identification in both fragments poses no difficulty, occurs a strongly convex vein (note that Fig. 1b reproduces the negative imprint) in both fragments. According to the branching pattern of this vein in the median and distal fragments, it is R. This identification is consistent with its observed convexity and its location in the basal fragment. In the basal fragment a concave, forked vein occurs immediately posterior to R. Posterior to this forked vein occurs a strongly convex vein (* on Fig. 1a, b), followed by a concave vein (° on Fig. 1a, b). They are separated by a narrow area. Posterior to vein ° occurs a broader area. In the median fragment a convex vein (1) (* on Fig. 1a, b) provided with an anterior concave vein, separated from a concave vein (2) by a narrow area, occur. A broad area occurs posterior to the vein (2) (° on Fig. 1a, b). Based on these similarities, the vein (1) is identified as vein *, and vein (2) as vein °. Therefore the forked vein occurring in the basal fragment is the base of M (or the base of the stem of M free from CuA, see below), as identified in the median and distal fragments.

The reconstruction of the wing venation of the holotype of *reliquia* n. sp. is not evident (see above), so is its interpretation, in relation to the taxonomic assignment of the species. The significance of our conclusion requires a detailed discussion.

First the cross-venation arranged in an archedictyon distinguishes *reliquia* n. sp. from nearly all insects of all time periods but palaeodictyopterans, known only during the Palaeozoic [Carpenter 1992; Belayeva et al. 2002; Grimaldi & Engel 2005; the identification of *gimmi* Kuhn, 1937 as a Mesozoic palaeodictyopteran by Bechly (1997) has been rejected by Willmann (2008)]. In addition, in *reliquia* n. sp., at least one concave vein occurs posterior to the concave vein indicated by ° on Fig. 1a, b. The latter being most likely (part of) CuP, it is assumed that the former also belong to this vein sector. Therefore CuP is branched in *reliquia* n. sp., a condition shared with – some – palaeopterans, and *Archaeorthoptera* and its precursors.

No intercalary secondary veins, with a relief opposed to that of surrounding main veins, diagnostic of odonatopterans, occur in *reliquia* n. sp. The species has neither a connection of MA with RP (or evidence of it) nor intercalary secondary veins diagnostic of ephemeropterans. Relationships with other palaeodictyopteroidean orders can be excluded based on the cross-venation: neither megasecopterans nor diaphanopterodeans and permothemistidans have reticulated crossveins (Carpenter 1992). In addition these insects have a connection or fusion of MA with RP in fore- and hind wings (when present), absent in *reliquia* n. sp. Therefore relationships with palaeopterans other than palaeodictyopterans can be excluded.

Assuming that the holotype of *reliquia* n. sp. is a hind wing, the fan-shaped posterior area is significantly smaller than that of Permian and Triassic *Archaeorthoptera* (and most polyneopterans of any period, Grimaldi & Engel 2005; in addition one would need to assume that it is foldable, as in polyneopterans, which is not evident from the available material). Assuming that the holotype is a forewing, it lacks the 'precostal' area diagnostic of orthopterans (Sharov 1968, 1971). In addition, in Palaeozoic and more recent orthopterans the area between the anterior wing margin and ScP tapers gradually, and/or ScP is branched, and/or RA is branched (Sharov 1968, 1971), unlike in *reliquia* n. sp.

In addition to these arguments, *reliquia* n. sp. is not a plecopteran as the median vein has more than two branches, a feature diagnostic of the group according to Béthoux (2005). It is unlikely a blattodean (including isopterans), as it has differentiated RA and RP, lacking in forewings of Permian and more recent representatives of the group (Carboniferous stem-blattodeans exhibiting a differentiated RA and RP also have a RA abundantly branched, unlike *reliquia* n. sp.). Relationships with 'basal' mantodeans are excluded because of the simple RA and/or the lack of connection of RP with M (see Béthoux & Wieland 2009). All dictyopterans have a simple CuP, suggesting that the holotype of *reliquia* n. sp. is not a hind wing of a representative of this group.

Relationships with paraneopterans can be excluded because of the long ScP and RA (Carpenter 1992). The long ScP and the comparatively low number of main vein branches exclude relationships with neuropterans (Carpenter 1992). The vein ScP is branched and/or short in most mecopterans (Carpenter 1992), unlike in *reliquia* n. sp. The comparatively abundant number of vein branches suggests that it is – obviously – not a hymenopteran, a dipteran, a coleopteran, or a strepsipteran. Finally, affinity with the enigmatic Carboniferous paoliidans (see a review in Prokop & Nel 2007) can be excluded based on the simple CuA (branched in both wing pairs in paoliidans; Kukalová 1958) and the branched CuP (simple in paoliidans). In addition *reliquia* n. sp. lacks the veinlets vanishing as crossveins, typical of paoliidans.

Based on its combination of character states, we conclude that *reliquia* n. sp. is most likely a palaeodictyopteran, although no definitive apomorphy was identified. Interpreting its wing venation in the light of this assignment requires some additional hypotheses. The vein we interpret as MA is concave, while it is convex in palaeodictyopterans. Whether the convexity of this vein has been altered, or it is not MA, is unknown. The vein indicated by * on Fig. 1a, b and described as CuA above is convex. Two concave branches diverge anteriorly from it. Considering that many palaeodictyopteran families have anterior vein sectors simple (Béthoux et al. 2007), we suggest that branches of MP are fused for some distance with CuA in *reliquia* n. sp. This interpretation is consistent with the observed veins relief. To our knowledge, such feature is unknown in (other) palaeodictyopterans.

The species *reliquia* n. sp. does not exhibit a fusion of ScP with RA, reported in all Middle (and Late?) Permian representatives of the group (Sinitshenkova 1992, 2002; Béthoux et al. 2007). It also lacks the elaborated complex of vein – crossveins fusions diagnostic of calvertiellidaean wing bases (Carpenter 1992; Béthoux et al. 2007). The absence of these features, assumed to be derived, indicates that distinct lineages, rooting from Late Carboniferous or Early Permian groups, persisted during the Middle (and Late?) Permian. However the distinctiveness of *reliquia* n. sp. and the lack of information on this species (e. g. morphology of the other wing pair), coupled with the lack of appropriate diagnoses for many existing palaeodictyopteran taxa, renders premature any attempt to assign *reliquia* n. sp. more precisely.

According to Dobruskina (1995; followed by Shcherbakov 2008), the Dzaylyaucho locality, from which the holotype of *reliquia* n. sp. has been unearthed, is Ladinian-Carnian in age (late Middle to early Late Triassic). Therefore *reliquia* n. sp. is the first palaeodictyopteran known from Triassic. Despite abundant collects in Dzaylyaucho, no representative of the group has been unearthed to date (Shcherbakov 2008). Our discovery indicates that the group survived the Permian/Triassic crisis as a relict.

Yet, during the middle (and Late?) Permian, the diversity of palaeodictyopterans declined, as indicated by their low species diversity (Sinitshenkova 2002). Therefore, it can be expected that a relict representative of the group could be discovered only after substantial collecting efforts in a Triassic outcrop. At the moment, it is unclear whether high latitude, mountainous, humid to semi-humid, and densely vegetated areas, such as the one surrounding the lake whose sediments yielded *reliquia* n. sp. (Voigt et al. 2006; Voigt et al. 2007), acted as a refuge for the group, or if palaeodictyopterans persisted as a relict group on a broader range during the Triassic.

3. Conclusion

Despite abundant previous collects (Shcherbakov 2008) the discovery of a palaeodictyopteran indicates that new collecting efforts are necessary before the composition of the Dzaylyaucho entomofauna could be known with appropriate detail. In addition, many species are known from a limited number of specimens, impeding analysis of intra-specific morphological variability. Such information would be essential for better delimit species and investigate community characteristics. On a broader perspective, the discovery of *reliquia* n. sp. might indicate that instead of experiencing extinction a number of Palaeozoic insect groups might have migrated to higher latitudes, where humid conditions prevailed during the Permian-Triassic aridisation of the palaeo-equatorial belt.

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Appendix

Genus *Liquia* n. gen.

Typus generis: *Liquia reliquia* n. sp.

Derivatio nominis: Random association of letters based on ‘reliquia’.

Diagnosis. – Same as type-species (see above).

Discussion. – There is no known palaeodictyopteran genus with a fusion of some branches from M with CuA, as in the type-species. Therefore the erection of a genus is justified.

Liquia reliquia n. sp.

Fig. 1

Holotypus: Specimens FG 596/IV/120a (negative imprint) and FG 596/IV/120b (positive imprint).

Derivatio nominis: After ‘relic’ in Latin.

Stratum typicum: “Upper Grey-coloured Member” (T4), Madygen Formation (Ladinian/Carnian, late Middle to early Late Triassic, according to DOBRUSKINA 1995).

Locus typicus: Sharov quarry (No. 14; DOBRUSKINA 1995), northwestern Madygen outcrop area (Urochishche Dzaylyaucho), Batken district (Oblast), southwest Kyrgyzstan.

Diagnosis. – RA, MA, and CuA simple; branches of MP fused with CuA and diverging anteriorly from it; five transversal dark stripes.