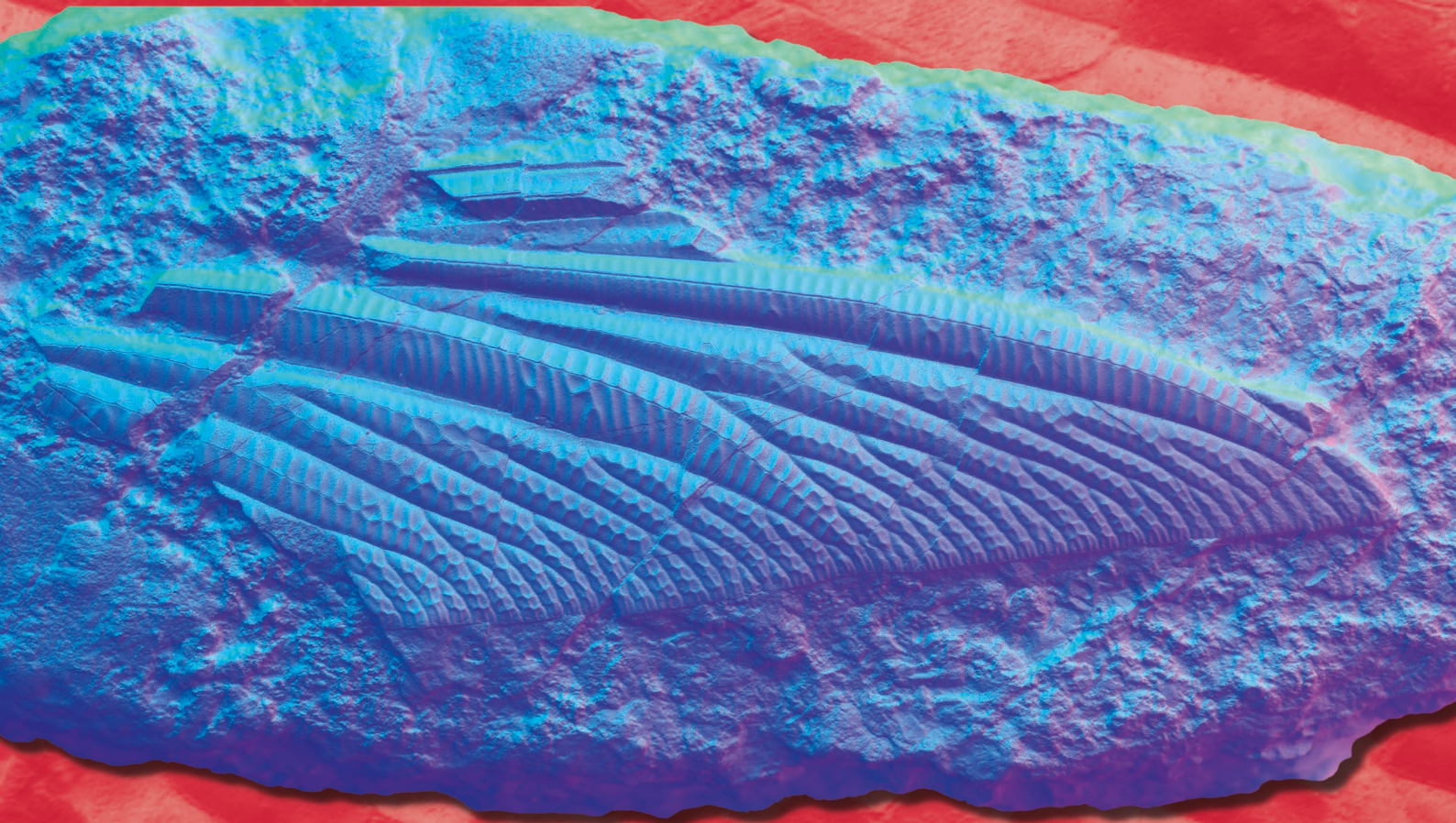


New light shed on Triadophlebiomorpha
wing morphology and systematics
(Insecta: Odonata)

Olivier BÉTHOUX &
John M. ANDERSON



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COUVERTURE / *COVER* :

Aile de *Reisia gelasii* (Reis, 1909) en visualisation des normales (holotype, spécimen SNSB-BSPG 1908 I 49)
Wing of Reisia gelasii (Reis, 1909) under normals visualisation (holotype, specimen SNSB-BSPG 1908 I 49)

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New light shed on Triadophlebiomorpha wing morphology and systematics (Insecta: Odonata)

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ABSTRACT

The systematics of the Triadophlebiomorpha, a group of often large-sized stem-Odonata, essentially Triassic, is reconsidered based on new data on some of the known species and on new material from the Molteno Formation (South Africa). New data on *Reisia gelasii* (Reis, 1909) (Anisian; Muschelkalk basin, Germany) and ‘*Triadotypus guillaumei*’ Grauvogel & Laurentiaux, 1952 (Anisian; Grès à Voltzia, France) allowed reconsidering the delimitation of the corresponding genera, *Reisia* Handlirsch, 1912 and *Triadotypus* Grauvogel & Laurentiaux, 1952, the latter regarded as a junior synonym of the former. Thanks to its pristine preservation of the wing three-dimensional structure, the material of *Piroutetia liasina* Meunier, 1907, re-illustrated, provides further insights on wing venation homologies in the group. These new data, coupled with new ones on known and new material from Molteno (Carnian; Karoo Basin, South Africa), led us to corroborate the placement of *Triassologus biseriatus* Riek, 1976 to the Triadophlebiomorpha, and to recognize ‘*Reisia rieki*’ Deregnacourt, Wappler, Anderson & Béthoux, 2017 as its junior synonym. In turn, it is argued that the sub-contemporaneous species *Iverya aveyri* Béthoux & Beattie, 2010, from Australia, is to be assigned to *Triassologus* Riek, 1976 (and the genus *Iverya* Béthoux & Beattie, 2010 considered its junior synonym), further emphasizing similarities between South African and Australian Triassic insect faunas. A subset of the Triadophlebiomorpha possesses a CuP+AA stem splitting into CuA and CuP+AA (as opposed to Cu and AA). This trait is present in *Nototriadophlebia pritykinae* n. gen., n. sp., an addition to the Triadophlebiomorpha from Molteno.

KEY WORDS

Fossil insect,
Triassic,
revision,
RTI,
Molteno,
new synonyms,
new combinations,
new genus,
new species.

RÉSUMÉ

Un nouvel éclairage sur la morphologie alaire et la systématique des Triadophlebiomorpha (Insecta, Odonata). La systématique des Triadophlebiomorpha, un groupe d'odonates souches de taille souvent importante, essentiellement triasiques, est reconsidérée d'après de nouvelles données sur certaines des espèces connues et sur du matériel inédit de la Formation Molteno (Afrique du Sud). Les nouvelles données sur *Reisia gelasii* (Reis, 1909) (Anisien; bassin du Muschelkalk, Allemagne) et '*Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952 (Anisien; Grès à Voltzia, France) permettent de reconsidérer la délimitation des genres correspondants, *Reisia* Handlirsch, 1912 et *Triadotypus* Grauvogel & Laurentiaux, 1952, le dernier vu comme le synonyme plus récent du premier. Grâce à l'excellente préservation de la structure tri-dimensionnelle de l'aile, le matériel de *Piroutetia lasina* Meunier, 1907, réillustré, fournit des informations supplémentaires sur les homologies de nervation des ailes chez le groupe. Ces nouvelles données, couplées à d'autres sur du matériel connu et inédit de Molteno (Carnien ; bassin du Karoo, Afrique du Sud), nous amènent à corroborer le placement de *Triassologus biseriatus* Riek, 1976 chez les Triadophlebiomorpha, et à reconnaître '*Reisia rieki* Derognaucourt, Wappler, Anderson & Béthoux, 2017 comme son synonyme plus récent. À la suite de quoi il est avancé que l'espèce sub-contemporaine, *Iverya aveyri* Béthoux & Beattie, 2010, d'Australie, doit être attribuée à *Triassologus* Riek, 1976 (et le genre *Iverya* Béthoux & Beattie, 2010 considéré comme son synonyme plus récent), soulignant plus avant les similitudes entre les faunes d'insectes du Trias sud-africain et australien. Un sous-ensemble de Triadophlebiomorpha possède une branche CuP+AA se divisant en CuA et CuP+AA (et non pas Cu et AA). Ce trait est présent chez *Nototriadophlebia pritykinae* n. gen., n. sp., un ajout aux Triadophlebiomorpha de Molteno.

MOTS CLÉS

Insecte fossile,
Trias,
révision,
RTI,
Molteno,
synonymes nouveaux,
combinaisons nouvelles,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The Triassic record of stem-relatives of dragon- and damselflies (Odonata), though limited compared to Permian and Jurassic ones, yet indicates that these insects evolved very divergent morphotypes at the time (Derognaucourt *et al.* 2023). Besides the rare Panodonata, the taxon including crown-Odonata and represented by mid-sized species at the time (Bechly 1997; Nel *et al.* 2002; Pritykina 1981; Tierney *et al.* 2020), the gracile, damselfly-like type was represented by the Archizygotera (Bechly 1997; Derognaucourt *et al.* 2021b; Felker 2022; Nel *et al.* 2005; Pritykina 1981). Besides these two taxa, the Triadophlebiomorpha, a group almost exclusively Triassic, included the most large-sized odonatans of the time and evolved a number of peculiar structures, such as a very large area between RP3+4 and MA, a very long petiole, and a number of distinctive vein fusions (Pritykina 1981; Nel *et al.* 2001; Béthoux *et al.* 2009; Béthoux & Beattie 2010; Derognaucourt *et al.* 2017, 2021a; Zheng *et al.* 2017a, b; Jouault *et al.* 2023). However, resulting from the combination of a large size and relative rarity (as expected from presumed top predators), most Triadophlebiomorpha species are known from few and/or incomplete wings. Moreover, many of the known species are documented based on material from the Madygen locality, which endured severe deformation (Voigt *et al.* 2017; and references therein). Finally, several of the earliest known representatives have never been revised in the light of more recent discoveries, or even never definitely identified as members of this group (see below). This situation makes the systematics of the group arduous. In the following, based on a wide corpus of data on some of the known species and on new material, we discuss some points of wing venation homology relevant to the whole Triadophlebiomorpha and then address aspects of the group systematics.

MATERIAL AND METHODS

FOSSIL MATERIAL

We gather data on material housed in a number of different institutions whose acronyms (or collection acronyms) are as follows:

AM	Australian Museum, Sydney, Australia;
MNHN.F	Palaeontology collection, Muséum national d'Histoire naturelle, Paris, France;
SMNS	'Staatliches Museum für Naturkunde Stuttgart', Stuttgart, Germany;
SNSB-BSPG	'Bayerische Staatssammlung für Paläontologie und Geologie', Munich, Germany;
PRE/F/ and BP/2/	Anderson collection, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa;
PIN	Borissiak Paleontological Institute, Moscow, Russian Federation.

DATA ACQUISITION AND PREPARATION

New photographs reproduced on Figs 1-3 were taken using a digital camera Canon EOS 5DS; those reproduced on Figs 4, 5, 6A, 7-9 were taken using a digital camera Canon EOS 5D Mark III (the photograph composing Fig. 6B is reproduced from Béthoux & Beattie 2010); the photograph reproduced on Fig. 10 was provided by a colleague using an unspecified equipment. Camera bodies were coupled to a Canon 50 mm or Canon MP-E 65 mm macro lens (all Canon, Tokyo, Japan; equipped with a polarizing filter), as applicable. In the case of the holotype of '*Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952 (Fig. 2B, E) the embedding rock was used as reference for white balance. Unless specified, photographs were taken under dry conditions. Photograph optimization was performed using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA,

United States). The photograph reproduced as Fig. 4E is a patchwork of two, dry-ethanol composite photographs (see below), specifically: i) of the specimen side preserving the wing in dorsal aspect (side 'a'), flipped horizontally (most of left portion); and ii) of the specimen side preserving the wing in ventral aspect (side 'b'), light-mirrored (right portion and small portion of the posterior wing margin opposite the pons). Photographs reproduced as Fig. 8B, D were obtained by merging a pair of photographs, one taken under dry condition, the other with the specimen cover with a thin film of ethanol ('dry-ethanol composites'). On the photograph reproduced as Fig. 8D, the glued fragments composing the specimen are readjusted digitally.

Besides traditional photography, the specimens 'SMNS Grauvogel collection 7885' (wing base; holotype of '*Triadotypus guillaumei*'), the specimen SNSB-BSPG 1908 I 49 (holotype of *Reisia gelasii* (Reis, 1909)) and the specimen MNHN.F.B09711 (holotype of *Piroutetia liasina* Meunier, 1907) were also documented using Reflectance Transforming Imaging (RTI; see, among others, Béthoux *et al.* 2016, Earl *et al.* 2010, Hammer *et al.* 2002). The corresponding RTI files are publicly available from Béthoux & Anderson (Appendix 1). Each was derived from a set of 54 photographs obtained using a light dome of about 30 cm in diameter and equipped with the same number of LEDs (because of the expansion of the MP-E 65 mm macro lens inside the dome, only 47 photographs were useful in the case of the wing base of the holotype of '*Triadotypus guillaumei*'). Both the light dome and camera (as above-mentioned) were driven by a control box. Obtained images were then batch-optimized using Adobe Photoshop CS6 and were further compiled into an RTI file using the RTI Builder software v.2.0.2 using the HSH fitter (software freely available from Cultural Heritage Imaging). The holotype of *Piroutetia liasina* is crossed by a fault filled with calcite. As a consequence, the two sides mismatch. In order to ease comparison with other taxa, they were readjusted digitally prior to the computation of the RTI file, as part of the batch-optimization.

Hand-made draft drawings of complete specimens, or of some particular areas only, were produced with the aid of a microscope equipped with a camera lucida (Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10×/23 eye pieces, a Plan Apo S 1.0× FWD objective; all Zeiss, Jena, Germany). Drawings were finalized using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, United States) using both hand-made draft drawings and photographs (traditional and/or extracted from RTI files), composing distinct layers of the working document. Portions of wing venation which were reconstructed are faded.

WING VENATION TERMINOLOGY AND HOMOLOGIES

Within the framework of the serial insect wing venation ground-plan (Lameere 1922, 1923), we essentially follow topographic homology conjectures proposed by Riek & Kukalová-Peck (1984; and see Bechly 1996, Jacquelin *et al.* 2018), with few alterations. Notably, following Deregnau-court *et al.* (2021a), the first vein-like structure bridging MA

and MP is referred to as the 'pons' (elsewhere often termed 'MAB'). Adopted abbreviations are repeated for convenience (with mention of color-coding, where applicable):

AA	anterior Analis;
CuA	anterior Cubitus (green);
CuAprlg	prolongation of anterior Cubitus;
CuP	posterior Cubitus;
I	intercalary;
Irp ₁ -rp ₂	intercalary between RP1 and RP2 (orange);
Irp ₁₊₂ -rp ₃₊₄	intercalary between RP1+2 and RP3+4;
Icua	intercalary between CuA branches;
I-	concave intercalary;
I+	convex intercalary;
MA	anterior Media (red);
MP	posterior Media;
RA	anterior Radius (blue);
RP	posterior Radius (blue);
RP1+2	anterior branch of RP;
RP1	anterior branch of RP1+2;
RP2	posterior branch of RP1+2;
RP3+4	posterior branch of RP;
ScP	posterior Subcosta;
Sn	subnodus;
-	structure with concave elevation;
+	structure with convex elevation;
0	structure with neutral elevation.

Among extant dragonflies, some taxa exhibit 'supplementary' longitudinal structures crossing main vein branches and/or intercalaries, and which are derived from cross-venation. These have been traditionally labelled 'Rspl' and 'Mspl', and are both concave. Both are located between a convex (Irp₁₊₂-rp₃₊₄, and MA, respectively) and a concave structure (RP3+4, and MP). The structure labelled 'IMA' in the Palaeozoic stem-Odonata Protanisoptera (see Huguet *et al.* 2002; among others) is probably of the same nature. These supplementaries tend to blur the origin of main vein branches and/or intercalaries they cross, especially if they run closely alongside the main vein/intercalary immediately anterior to them. Based on this observation and new data (see below), we submit that a series of I+, and cross-veins bridging them, might form a prolongation of CuA running alongside MP, and crossing posterior branches of this vein. We propose the label 'CuAprlg' for this hypothetical structure.

It has been very generally considered that RP3+4 is dichotomously branched in species herein assigned to the Triadophlebiomorpha, with a distinction between 'RP3' and 'RP4' made in some accounts. This interpretation is justified by the angle made by this vein and its (presumed) branches at the (presumed) first fork. However, the possibility that this configuration evolved from a simple RP3+4 complemented by numerous posterior I- and I+, or a RP3+4 posteriorly pectinate and a complementary set of I+, is to be discussed. A relevant analogue is the organisation of the venation in the MA-MP area in large-sized Meganisopterans (see Zes-sin 1983; Nel *et al.* 2009; Li *et al.* 2013; Béthoux *et al.* 2021). Here the vein-like structure immediately anterior to MP is convex (as is MA) and is usually branched before its mid-length; while the more distal part of the MA-MP area is filled with a regular alternation of convex and concave veins, generally simple. All these structures have been

regarded as either intercalaries (for both concave and convex elements) or regular posterior branches of MA (convex) and intercalaries (concave). In other words, the first posterior, branched vein-like structure has never been regarded as a main branch of MA.

The triadophlebiomorphan *Sinotriadophlebia lini* Zheng, Nel & Zhang in Zheng *et al.* (2017a) displays a very similar configuration for the area between RP3+4 and MA. There is no obvious angle formed by RP3+4 opposite the point of divergence of 'its' first concave posterior structure (see original description). In other words, RP3+4 is either simple and with posterior intercalaries, or posteriorly pectinate. Cases known among triadophlebiomorphans provide a complete grade from a regular bending of RP3+4 to a more angulate course: RP3+4 is moderately angulate opposite the first concave intercalary/posterior branch in *Reisia gelasii* (Fig. 1) and '*Triadotypus*' *guillaumei* (Fig. 2), while it is sharply angulate in *Piroutetia liasina* (Fig. 3). The evolution of wing venation of Odonata is replete with cases where the course of a main vein gains a sharp angle when connected to a specialised cross-vein/intercalary, the first of these being MA when connected to the pons.

In the putative sister-groups of Triadophlebiomorpha, namely the megalisoptera, the Protanisoptera and early representatives of Stigmoptera, the area between RP3+4 and MA remains narrow, at least for most of its course, and is filled with a single row of cells (with rare exceptions; Zessin 1983; Huguet *et al.* 2002; Nel *et al.* 2012, 2009; Li *et al.* 2013; Béthoux *et al.* 2021 among others). From such a condition, it can be reasonably conceived that the broadening of the area between RP3+4 and MA, in yet unknown early relatives of Triadophlebiomorpha, induced the formation of intercalaries. Further broadening of the corresponding area led to a configuration similar to that of the MA-MP area in megalisoptera, with a first intercalary being branched, others arising as simple stems (or with more distal forks). Adopting this scenario implies that RP3+4 is simple, or posteriorly pectinate, in Triadophlebiomorpha (in any case it has a single main stem). The first proposal is favoured in the following.

Nel *et al.* (2001) reported the occurrence of a RP+MA common stem in '*Triadotypus*' *guillaumei*, but the occurrence of this trait could not be confirmed (see below). Similarly, according to Deregnacourt *et al.* (2017), *Triassologus biseriatus* (therein, '*Reisia rieki*') possesses a long RP+MA common stem distal to the pons. However, new material described below reveals that it is not the case, RP and MA being very close but distinct. Also, according to the reconstruction given by Zheng *et al.* (2017b) of *Sinotriadophlebia lini* (fig. 2), a long RP+MA stem occurs in this species, but this is contradicted by detailed photographs published by these authors (fig. 3C), on which RP and MA ('MA' therein) are distinct. Because the two veins commonly run very close (basal to the nodus) in triadophlebiomorphans, it is possible that MA, strongly convex, could partly overlap a strongly concave RP (and vice versa if the wing is viewed ventrally), rendering both veins difficult to distinguish. In summary, a RP+MA long common stem (distal to the pons) likely does not occur at all in triadophlebiomorphans.

Further aspects of wing venation homologies will be discussed within the 'Systematic Palaeontology' section with reference to particular specimens.

SYSTEMATIC PALAEONTOLOGY

All taxa considered below belong to the taxon Discoidalia Bechly, 1996, itself belonging to the order Odonata Fabricius, 1793. The sequence of species (re-)description was prompted by their relevance.

Order Odonata Fabricius, 1793

DISCOIDALIA Bechly, 1996

TRIADOPHLEBIOMORPHA Pritykina, 1981

EMENDED DIAGNOSIS. — Pons long and oblique; area between RP3+4 and MA generally broad, with a first posterior concave intercalary (I-) seemingly emerging from RP3+4, generally branched (with exceptions; alternatively worded 'RP3+4 seemingly branched').

COMPOSITION. — The super-families Triadophlebioidea (including the families Triadophlebiidae, Mitophlebiidae and Sinotriadophlebiidae; and the genus *Nototriadophlebia* n. gen. newly described herein, whose familial affinities remain uncertain) and Zygophlebioidea (including the families Zygophlebiidae and Xamenophlebiidae); and the genera *Reisia* Handlirsch, 1912, *Piroutetia* Meunier, 1907 and *Triassologus* Riek, 1976 as delimited herein, of uncertain super-familial affinities (see Pritykina 1981; Bechly 1996; Nel *et al.* 2001; Zheng *et al.* 2017b).

REMARKS

How the main taxa of Triadophlebiomorpha relate requires a specific discussion in the light of our new data on several key taxa. Nel *et al.* (2001); and see Zheng *et al.* 2017b) excluded the Triadotypidae Grauvogel & Laurentiaux, 1952 (the only family composing the taxon Triadotypomorpha Bechly, 1996) from the Discoidalia, while most other Triassic taxa displaying a seemingly branched RP3+4 were assigned to the Triadophlebiomorpha, within Discoidalia. This proposal essentially rested on the presumed lack of a pons in representatives of the Triadotypidae (Nel *et al.* 2001; and see Grauvogel & Laurentiaux 1952). However, our new investigation of the type species of the type genus of the family, namely '*Triadotypus*' *guillaumei*, reveals that it possesses a pons (see below and Fig. 2), and is therefore a Discoidalia. In addition, this pons is very long and oblique, a trait regarded by Bechly (1996), followed by Nel *et al.* (2001), as diagnostic of the Triadophlebiomorpha. Three other species where assigned by Nel *et al.* (2001) to the Triadotypomorpha (namely, '*Triadotypus*' *nana* Bechly, 1997, *Reisia gelasii* and '*Reisia*' *sogdianus* (Pritykina 1981), but the occurrence, or lack thereof, of a pons is unknown for these species (see original descriptions and revision of *Reisia gelasii* below). In summary the assumption that '*Triadotypus*' *guillaumei* lacks a pons led to an artificial splitting of taxa displaying a seemingly branched RP3+4.

A consequence is that the distinction between the taxa Triadophlebioptera Bechly, 1996, Triadotypomorpha Bechly, 1996 and Triadophlebiomorpha becomes unclear, the former suppos-

edly including the two latter. Characters listed as diagnostic of the Triadotypomorpha by Bechly (1996) were rightfully challenged by Nel *et al.* (2001). In turn, among those proposed by Nel *et al.* (2001) for the Triadotypidae/Triadotypomorpha, only the occurrence of a lobe-like anal area filled with AA veinlets (original formulation 'vein AA with several posterior branches, at least two of them being directed towards wing base') is peculiar to '*Triadotypus guillaumei*'. Moreover, the corresponding area is unknown in many triadophlebiomorphans herein regarded as closely related to this species. It will be considered below as of generic relevance. It might even represent a trait proper to the hindwing only. In summary, we propose to consider the taxa Triadophlebioptera and Triadotypomorpha obsolete, and resort only to Triadophlebiomorpha.

Apart from these aspects, the main framework of the inner systematics of Triadophlebiomorpha has been mainly unchanged since the contribution by Pritykina (1981). The family Paurphlebiidae was erected by Bechly (1996) based on the report, by Pritykina (1981), that ScP and RA are fused in a number of Triadophlebiomorpha from the Madygen locality. However, there is little doubt that this assumed fusion is a mere artefact due to: i) the fact that ScP, strongly concave, and R/RA, strongly convex, may overlap each other; and ii) extreme elongation experienced by the Madygen material. The new data provides limited relevant information on the position of two rather distinctive taxa, namely *Permophlebia uralica* Nel, Béthoux, Bechly, Martínez-Delclòs & Papier, 2001, known from the basal three-quarters of a single wing and the only representative of the Permophlebiidae, and *Kargalotypus kargalensis* (Martynov, 1932), known from the distal third of a single wing and transferred from Meganisoptera to Triadophlebiomorpha by Nel *et al.* (2001). They doubtlessly belong to the Triadophlebiomorpha, owing to the occurrence of a pseudo-forked RP3+4. These two poorly-known taxa might prove more closely related than currently assumed.

Genus *Reisia* Handlirsch, 1912

Reisia Handlirsch, 1912: 6. — Type species: see below.

Handlirschia Reis, 1909: 677.

Triadotypus Grauvogel & Laurentiaux, 1952: 124. — Type species: *Triadotypus guillaumei* Grauvogel & Laurentiaux, 1952.

Rabru Béthoux, De la Horra, Benito, Barrenechea, Galán & López-Gómez, 2009: 182. — Type species: *Rabru rubra* Béthoux, De la Horra, Benito, Barrenechea, Galán & López-Gómez, 2009, n. syn.

TYPE SPECIES. — *Handlirschia gelasii* Reis, 1909 by monotypy.

DIAGNOSIS. — RP1/RP2 fork and point of origin of the first I- in the area between RP3+4 and MA opposite each other, or nearly so (known in *Reisia gelasii*, *Reisia guillaumei* n. comb. and *Reisia rubra* n. comb.); pons very long (known in *Reisia guillaumei* n. comb. only); RP/MA fork in a more basal position than the MP/Cu+AA fork (known in *Reisia guillaumei* n. comb. only); at its origin, Irp₁-rp₂ closer to RP2 than to RP1 (known in *Reisia guillaumei* n. comb. and *Reisia rubra* n. comb.); first I- in the RP3+4 area well-developed, dichotomously

branched (known in all species); in its distal part, MP with 4 main posterior branches (in addition to the ending of its main stem; known in *Reisia gelasii* and *Reisia rubra* n. comb., assumed in *Reisia guillaumei* n. comb.; probably fewer branches in *Reisia rubra* n. comb.); in the area between the first and second posterior branches of CuA, occurrence of a well-developed, branched I- (known in *Reisia guillaumei* n. comb. and *Reisia rubra* n. comb.); CuP rectilinear (as opposed to curved or sigmoidal), with two main stems, both branched, with a well-formed I+ between them (known in *Reisia guillaumei* n. comb. and *Reisia rubra* n. comb.); AA (or, anterior branch of) rectilinear (as opposed to curved or sigmoidal; known in *Reisia guillaumei* n. comb. and *Reisia rubra* n. comb.); area between AA and the posterior wing margin, basal to the pons, lobe-shaped and filled with poorly organized veinlets, some directed backwards (known in *Reisia guillaumei* n. comb. only; possibly a feature proper to the hindwing).

OTHER SPECIES. — *Reisia guillaumei* (Grauvogel & Laurentiaux, 1952), n. comb., *Reisia nana* (Laurentiaux-Vieira, Ricour & Laurentiaux, 1952) and *Reisia rubra* (Béthoux, De la Horra, Benito, Barrenechea, Galán & López-Gómez, 2009), n. comb.

REMARKS

Whether a number of triadophlebiomorphan species should be included, or not, in this genus, remained a conundrum for decades due to the incompleteness of the available material on one hand, and inadequate data on some of its potential relatives. Preliminarily, in the holotype of *Reisia gelasii*, circular elevations with a puncture in their middle occur in the area between RP1 and RP2 [at least in its basal part; noted by Reis (1909) as 'pores'; see Fig. 1E, F]. This is unique among triadophlebiomorphans but might have been overlooked and/or may be poorly preserved in other members of this taxon. Indeed, similar structures were observed by Carpenter (1947) in Permian, large-sized Meganisoptera. According to this author, they might represent setal bases. The occurrence and distribution of these structures would need a better documentation for their systematic relevance to be properly assessed.

Our new data and observations led us to concur with Bechly (1997; and see Grauvogel & Laurentiaux 1952) that the genus *Triadotypus* Grauvogel & Laurentiaux, 1952 must be regarded a junior synonym of *Reisia* Handlirsch, 1912. Indeed, as far as preserved, the respective holotypes (and only known material) of the type-species of each genus (*Reisia gelasii* [Fig. 1] and '*Triadotypus guillaumei*' [Fig. 2]) are nearly identical, including size (width opposite the RP1/RP2 fork, 22.0 mm and about 22.4 mm, respectively), but for: i) the RP1/RP2 fork and the point of origin of the first I- in the RP3+4, both located in a slightly more basal position in *Reisia gelasii*; and ii) a higher density of cross-veins in the median part of the wing in *Reisia gelasii*. Such traits are best regarded as of specific relevance. Among characters advocated by Nel *et al.* (2001) to maintain *Reisia* and *Triadotypus* as distinct genera, only the branching pattern of MP (or lack thereof) is preserved in both holotypes. Even though the holotype of '*Triadotypus guillaumei*' is comparatively poorly preserved in the corresponding area, the course of the CuA distal-most branch suggests that MP indeed possesses genuine posterior branches, as in *Reisia gelasii*. Another notable point is that in '*Triadotypus nana*', consistently regarded as closely related to '*Triadotypus guillaumei*' by previous authors (including Nel *et al.* 2001), MP clearly has several posterior branches.

We further noted unexpected similarities between *Reisia guillaumei* n. comb. and ‘*Rabru rubra*. Even if the latter is known from a fragmentary, single wing, its wing venation matches, in nearly every aspect, that of *Reisia guillaumei* n. comb., including the organisation of CuP, provided with two main stems and an I+ between them. Both species are also very similar in size (width opposite the RP1/RP2 fork about 21.4 mm in ‘*Rabru rubra*). We therefore propose to assign ‘*Rabru rubra* to the genus *Reisia*. One notable point regards the number of MP and CuA branches, lower in *Reisia rubra* n. comb. than in any other species herein assigned to *Reisia*. This trait is considered as of specific relevance. As for *Reisia nana* (Laurentiaux-Vieira, Ricour & Laurentiaux, 1952), known from a very fragmentary, single wing, there are virtually no differences between it and *Reisia guillaumei* n. comb., apart from a distinctly smaller size (judging from the morphology of the latter, wing width is about 14.0 mm opposite the RP1/RP2 fork in *Reisia nana*), which justifies maintaining the species (Bechly 1997).

The assignment of ‘*Triadotypus sogdianus* Pritykina, 1981 to the genus *Reisia*, provisionally proposed by Nel *et al.* (2001), is dubious, as this species has (compared to *Reisia* species for which the corresponding traits are documented): i) the first fork of the first I- in the area between RP3+4 and MA area located more basally; ii) a more developed MP; and iii) curved CuP and AA. This species should probably be assigned to a genus on its own. The case of ‘*Reisia rieki* Deregnaucourt, Wappler, Anderson & Béthoux, 2017 will be addressed below.

In summary, available evidence points towards marked similarities between *Reisia gelasii*, *Reisia guillaumei* n. comb., *Reisia rubra* n. comb. and *Reisia nana*. Yet, it must be acknowledged that most of these species are known from fragmentary material. Future discoveries might reveal unforeseen differences, making it necessary to reinstate some of the genera herein regarded as junior synonyms of *Reisia*.

Reisia gelasii (Reis, 1909)
(Fig. 1)

Handlirschia gelasii Reis, 1909: 694, figs 1-7.

Reisia gelasii – Handlirsch 1912: 6. — Schmidt 1928: 329, fig. 903. — Grauvogel & Laurentiaux 1952: 128, fig. 5. — Laurentiaux 1958: 37 (*partim*) — Bechly 1997: 53 (*partim*). — Nel *et al.* 2001: 507, fig. 4.

EXAMINED MATERIAL. — Holotype and only known specimen SNSB-BSPG 1908 I 49 (right wing in dorsal aspect; ‘Bayerische Staatssammlung für Paläontologie und Geologie’, Munich, Germany; Fig. 1).

TYPE LOCALITY AND STRATIGRAPHY. — Műnnerstadt, Germany; Muschelkalk basin, Schaumkalkbänke Member, Jena Formation; Anisian, Triassic (Paleobiology Database; Nel *et al.* 2001).

EMENDED DIAGNOSIS. — Width opposite the RP1/RP2 fork about 22 mm (lower in *Reisia nana*); in the area delimited anteriorly by RP2 and posteriorly by the first I- between RP3+4 and MA, approximately in the median area of the wing (between the ori-

gin of the first I- in the RP3+4 and its first fork), cross-venation denser than in surrounding areas (autopomorphic trait); MP with 4 main posterior branches (in addition to its anterior stem; lower in *Reisia rubra* n. comb.).

REMARKS

Among triadophlebiomorphans, the comparatively high density of cross-veins in the median area of the wing is unique. We submit that it is relevant to distinguish *Reisia gelasii* from other *Reisia* species (area poorly known in *Reisia rubra* n. comb., but which has fewer MP and CuA branches; area unknown in *Reisia nana*, which is distinctly smaller).

There is little to add to the original description by Reis (1909) of the available material. Yet, the exceptionally well-preserved vein corrugation provides interesting clues on how intercalaries can mimic main veins. In the distal part of the RP3+4-MA area four pairs of convex and concave intercalaries (I+ and I-) arise from regularly convex cross-veins, close to RP3+4 (Fig. 1B, C; two of these pairs visible on Fig. 1C). More basally, a very similar pair of intercalary arises from a cross-vein which elevation can be considered neutral. Even more basally, the concavity typical of the I- of the pair applies to the cross-vein in connection with RP3+4. In other words, the I- of a pair of intercalaries adopts a vein-like origin. This case clearly supports the view that the apparent posterior (concave) branch of RP3+4 is more likely an extensively developed I-.

Another relevant aspect of wing venation homology for which the specimen provides some clues regards the number of MP vs CuA branches, a point that could be referred to as the ‘MP-CuA twilight zone’. In its distal part, MP is undoubtedly provided with three posterior branches (Fig. 1B, D; the most distal and most basal ones have a clear concave origin; only the most basal one of the three is visible on Fig. 1D). More basally, concave structures do not display such clear concave origin from MP. As for CuA, even though its basal stem is not preserved, it can be assumed from data on *Reisia guillaumei* n. comb. (Fig. 2) and *Piroutetia liasina* (Fig. 3) that it has two branches at least, probably more (in green on Fig. 1A). Then, the nature of structures encircled in white on Fig. 1D is not obvious. A first interpretation, favoured herein, predicts that a CuAprlg (see ‘Material and methods’ section) might begin to form, crossing one posterior branch of MP (which putative base is indicated by ‘0’ on Fig. 1D). This vein would then have a total of five main branches (four posterior branches in addition to the ending of its main stem), and CuA three preserved ones, and most likely four in total, as in *Reisia guillaumei* n. comb. A second interpretation predicts that CuA extends further, with a total of five main branches (four preserved and one inferred), and MP four (including its main stem). The case of *Piroutetia liasina* (Fig. 3), where no CuAprlg can be assumed, shows that CuA has fewer branches than MP (two vs three). We therefore favour the interpretation that, in *Reisia gelasii*, a CuAprlg occurs along a short section and that CuA most likely had four branches (three of which are preserved).

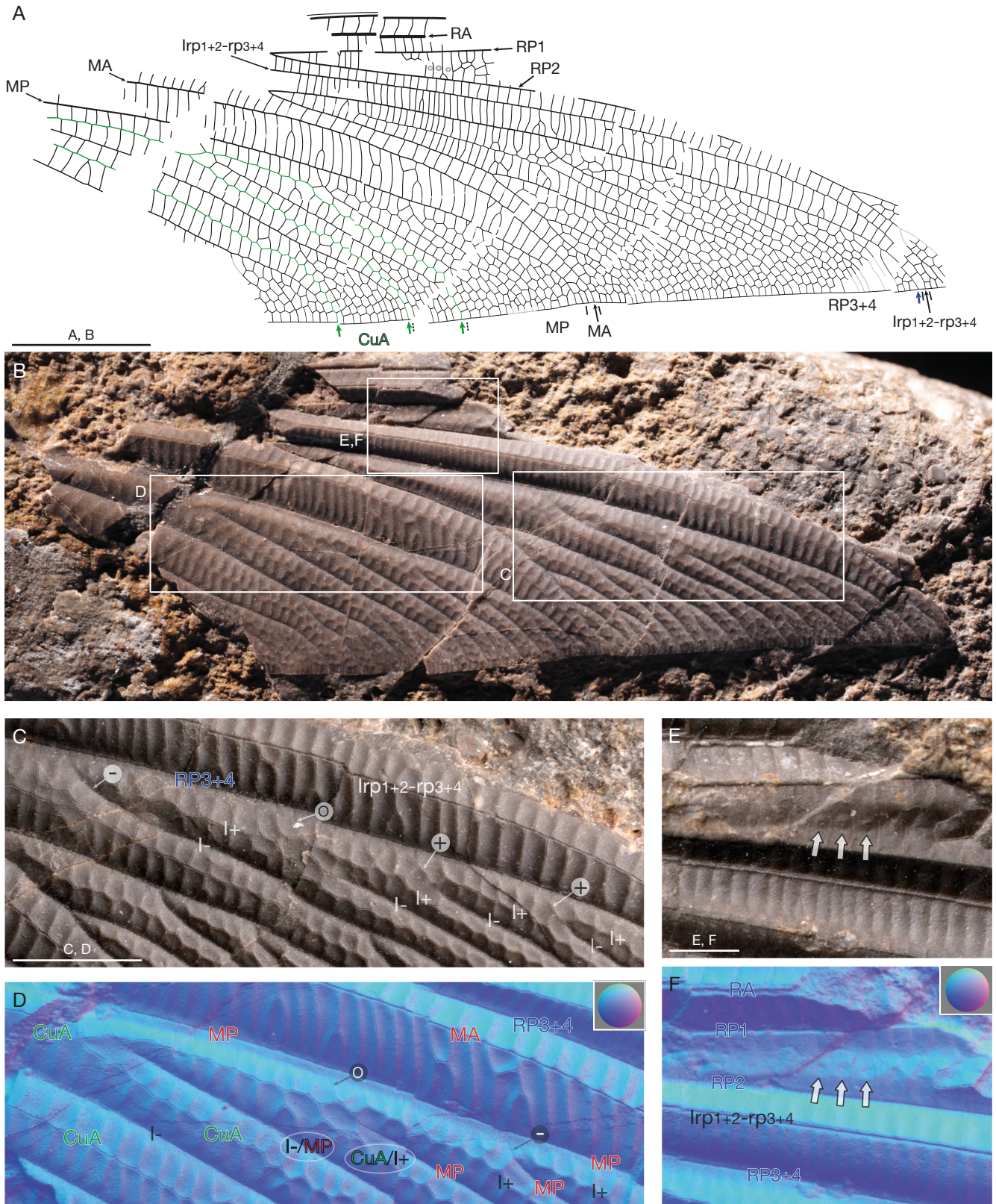


FIG. 1. — *Reisia gelasii* (Reis, 1909), holotype, specimen SNSB-BSPG 1908 I 49 ('Bayerische Staatssammlung für Paläontologie und Geologie', Munich, Germany), right wing in dorsal aspect: **A**, **B**, overview; **A**, drawing of venation (small blue arrow, ending of RP3+4; small green arrows indicating the termination of CuA branches); **B**, photograph; **C**-**F**, details, locations as shown on **B**, photographs extracted from RTI file (**D**, **F**, under normals visualisation); **C**, area posterior to RP3+4, the origins of paired convex and concave intercalaries (I+ and I-) become increasingly concave from the distal to the proximal areas; **D**, detail of the 'MP-CuA twilight zone' (nature of structures encircled in white discussed in the text); **E**, **F**, detail of presumed setal bases (large white arrows indicating the best preserved ones). Scale bars: A, B, 10 mm; C, D, 5 mm; E, F, 2 mm.

Reisia guillaumei

(Grauvogel & Laurentiaux, 1952), n. comb.

(Fig. 2)

Triadotypus guillaumei Grauvogel & Laurentiaux, 1952: 124, figs 2, 3. — Nel *et al.* 2001: 503, figs 1-3.

Reisia gelasii Laurentiaux, 1958: 37, text-figs 3, 4, pl. 1, fig. 2 (*partim*). — Bechly 1997: 53 (*partim*).

EXAMINED MATERIAL. — Holotype and only known specimen 7885/7886 (left wing in dorsal and ventral aspect, respectively; also referred to as '57.32' or '5732' in the literature; Louis Grauvogel collection at the 'Staatliches Museum für Naturkunde Stuttgart', Stuttgart, Germany; Fig. 2).

TYPE LOCALITY AND STRATIGRAPHY. — Bust (Bas-Rhin, France); 'Grès à Voltzia' Formation; Anisian, Triassic; Gall & Grauvogel-Stamm 2005).

EMENDED DIAGNOSIS. — Width opposite the RP1/RP2 fork about 22 mm (lower in *Reisia nana*); MP with 4 main posterior branches (in addition to its anterior stem; fewer branches in *Reisia rubra* n. comb.).

REMARKS

Our investigation revealed a number of discrepancies between previous descriptive accounts and what can be observed in the available material. Most importantly, the part that Nel *et al.* (2001) regarded as the base of MP (and Grauvogel & Laurentiaux [1952] as the base of CuP) turns out to be the pons, which is very long. Incidentally, it is strongly convex, which is inconsistent with an identification as (part of) MP. The course of the actual base of MP, although poorly preserved, yet is substantiated by a marked concave groove immediately posterior to the pons (black arrow on Fig. 2E, F). Additionally, there is no evidence of a long RP+MA stem, as suggested by Nel *et al.* (2001). The corresponding area is not preserved in the side preserving the wing in dorsal aspect (Fig. 2): only a very short section of the stem of RA (or R) is preserved, ending opposite the white arrow on Fig. 2E, F. The splitting plane then runs at the level of ScP, which is well exposed, with a short section of MA visible (i.e. RA and RP are embedded in the other side of the specimen). Further on, where preserved, RA (blue arrow on Fig. 1A, B), RP and MA are clearly distinct. Quite unfortunately the corresponding area is totally missing in the side preserving the wing in ventral aspect (7886), probably as a consequence of rock splitting at the time of collection. Given our current knowledge of the wing morphology in triadophlebiomorphans, it is rational to assume that RP and MA run next to each other, but distinct, in *Reisia guillaumei* n. comb. (Fig. 2A; and see above).

Genus *Piroutetia* Meunier, 1907

Piroutetia liasina Meunier, 1907

(Fig. 3)

EXAMINED MATERIAL. — Holotype and only known specimen MNHN.F.B09711 (left wing in ventral aspect; Muséum national d'Histoire naturelle, Palaeontology collection, Paris, France; Fig. 3).

REMARKS

The redescription of the holotype (and only known specimen) of this species by Nel (1989) only needs a minor emendation, regarding the occurrence of a cross-vein more oblique than others in the distal part of the RA-RP1 area. Such a cross-vein commonly occurs in Triadophlebiomorpha (Pritykina 1981).

The excellent preservation of veins corrugation in the specimen makes it particularly interesting. It can be assessed that MP is branched distally, posteriorly pectinate, with a total of 4 branches. The first posterior branch of MP as identified by Nel (1989) is herein regarded as an intercalary vein occurring between the two branches of CuA, which is more consistent with: i) the lack of a concave base in connection with MP; ii) the position of this structure relative to the most distal (genuine) MP branches; and iii) the common occurrence of such IcuA in Triadophlebiomorpha. The course of Irp₁-rp₂ (expected to be convex) is not evident if considering veins elevation: our proposal (Fig. 3A) supposes that it is alternatively convex and concave (Fig. 3B). A possible explanation is that Irp₁-rp₂ is fused with a posteriorly pectinate I- that would have occurred between Irp₁-rp₂ and RP2. Such a structured I- is known in *Cladophlebia parvula* Pritykina, 1981 (see original description), in which it seemingly originates from RP2. Moreover, it is separated from Irp₁-rp₂ by a very narrow area. A fusion of the two structures, as proposed herein for *Piroutetia liasina*, is therefore plausible.

Genus *Triassologus* Riek, 1976

Triassologus Riek, 1976: 793. — Type species: see below.

Iverya Béthoux & Beattie, 2010: 689 — Type species: *Iverya aveyri* Béthoux & Beattie, 2010, n. syn.

TYPE SPECIES. — *Triassologus biseriatus* Riek, 1976 by original designation.

OTHER SPECIES. — *Triassologus aveyri* (Béthoux & Beattie, 2010), n. comb.

EMENDED DIAGNOSIS. — Hindwing broader than forewing (1.3 broader opposite nodus); area between anterior wing margin (or ScA) and ScP very broad in forewing, moderately broad in hindwing; area between anterior wing margin and RA very narrow opposite the third quarter of wing length, before widening again (as opposed to tapering, or broadening, regularly from the nodus to the apex; uncertain in *Triassologus aveyri* n. comb.); nodal and sub-nodal cross-veins short, moderately strong, sub-aligned, oblique (condition unknown in *Triassologus aveyri* n. comb.); RP1/RP2 fork in a position more distal than that of the point of origin of the first I- in the RP3+4 area; first I- in the Irp₁-rp₂-RP2 area seemingly originating from RP2 (i.e. RP2 pseudo-forked; large blue arrows on Fig. 4B-D, F; unknown in *Triassologus aveyri* n. comb.); point of origin of the first I- in the RP3+4 area basal to the RP1/RP2 fork; RP3+4 very long, parallel to the posterior wing margin for some distance (unknown in *Triassologus aveyri* n. comb.); pons moderately long; RP/MA fork opposite that of MP/Cu+AA; at least in the basal part of the CuA-CuP area, I- rectilinear and seemingly originating from CuA (possibly as convex elements quickly turning concave; large white arrows on Fig. 6), genuine CuA branches zigzagging and seemingly originating from cross-venation (i.e. as an I+; large green arrows on Fig. 6; and see small green arrows on Figs 4D, 5B); CuP reaching

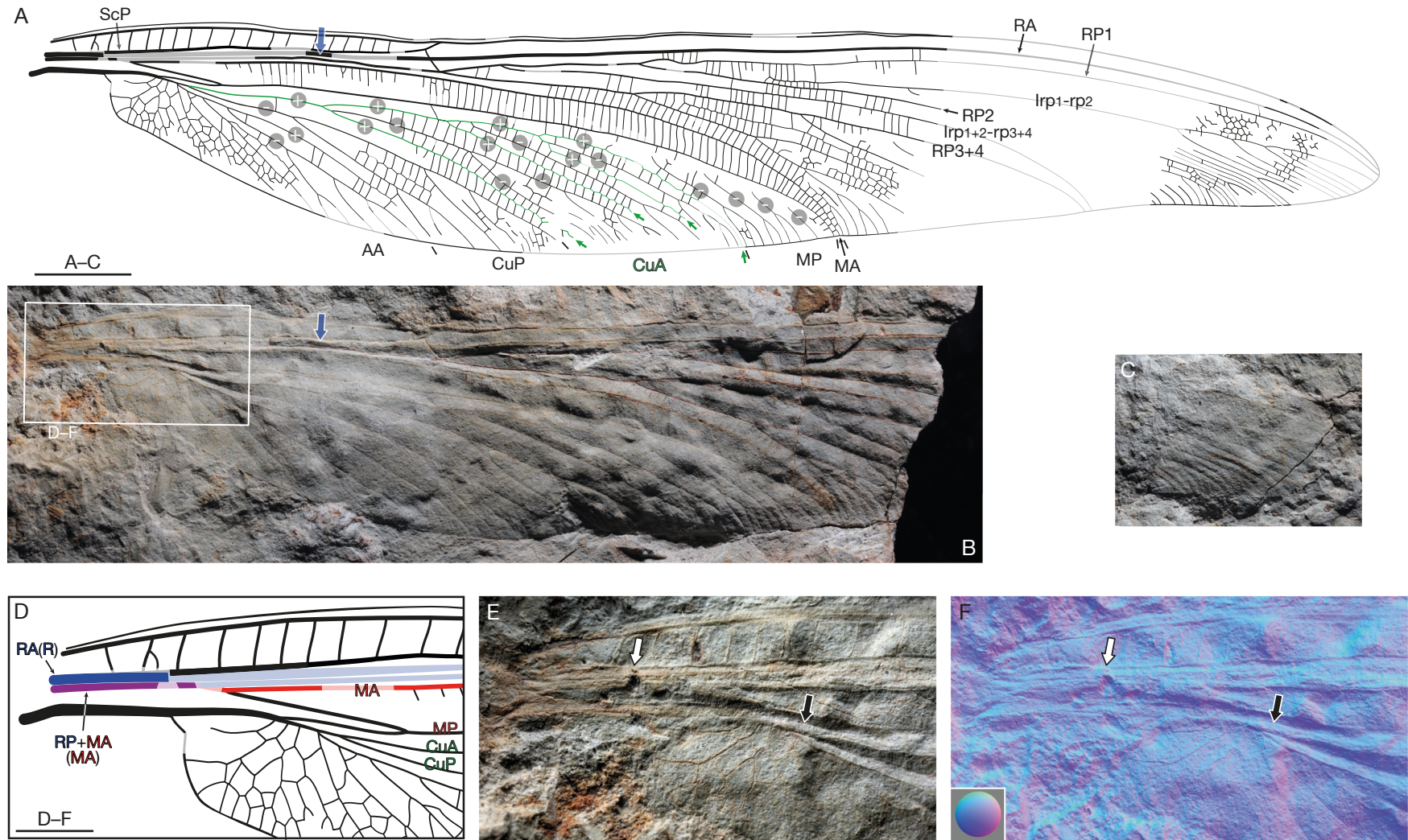


FIG. 2. — *Reisia guillaumei* (Grauvogel & Laurentiaux, 1952), n. comb., holotype, specimen 7885 (collection Louis Grauvogel at the 'Staatliches Museum für Naturkunde Stuttgart', Stuttgart, Germany), left wing: **A-C**, overview; **A**, drawing of venation (large blue arrow indicating the only portion of RA preserved between the pons and the nodus; small green arrows indicating the termination of CuA branches); **B**, photograph of the main fragment, dorsal aspect (flipped horizontally); **C**, photograph of the distal fragment, dorsal aspect (flipped horizontally); **D-F**, detail of the wing base, location as shown on **B**; drawing of venation (enlargement from **A**, with added color-coding); **E**, **F**, photographs extracted from RTI file (**F**, under normals visualisation; large white arrow indicating the end of the preserved section of the adjoined R and MA [or RA and RP+MA]; large black arrow indicating the course of MP below the pons). Scale bars: A-C, 10 mm; D-F, 4 mm.

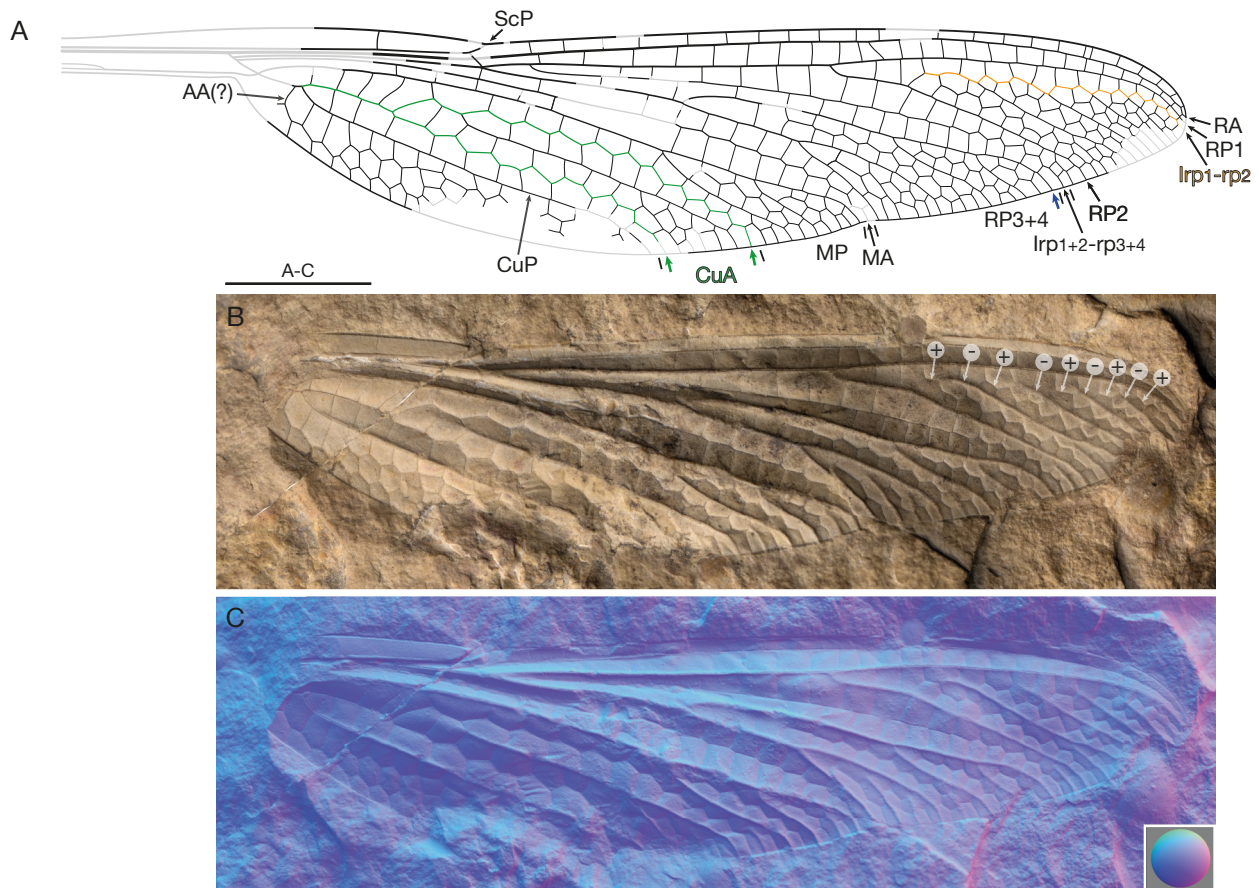


FIG. 3. — *Piroutetia liasina* Meunier, 1907, holotype, specimen MNHN.F.B09711: **A**, drawing of venation, with tentative reconstruction of wing base; **B**, **C**, photographs extracted from RTI file; **B**, light-mirrored; **C**, normals visualisation. Scale bar: 5 mm.

the posterior wing margin opposite the nodus or slightly distal to it; CuP and AA posteriorly pectinate, with a curved and sigmoid course, respectively; area between AA (or Cu+AA, or MP+Cu+AA) and the posterior wing margin, opposite and basal to the pons, narrow (i.e. not forming a lobe).

REMARKS

It will be shown below that ‘*Reisia*’ *rieki* Deregnaucourt, Wappler, Anderson and Béthoux, 2017 is a junior synonym of *Triassologus biseriatus* Riek, 1976. This could imply that *Triassologus* is a junior synonym of *Reisia*. However, new data derived from additional material of *Triassologus biseriatus* (see below) and on *Reisia* spp. (see above) allows to convincingly differentiate the two genera, including the width of the area between the anterior margin (or ScA) and ScP, and the particular organisation of I- and CuA branches in the CuA-CuP area, among others.

The more complete data on *Triassologus biseriatus* (see below) led us to compare it with the Australian Triassic species ‘*Iveryia*’ *aveyri* Béthoux & Beattie, 2010 (type species of the genus *Iveryia* Béthoux & Beattie, 2010). Indeed, as far as comparison can be made, the two species do not display major differences other than size-related ones, such as the overall number of vein branches (assuming that the only known specimen of ‘*Iveryia*’ *aveyri* is a forewing, it is about 1.4 times larger than in that of *Triassologus biseriatus*). We

therefore propose to newly assign ‘*Iveryia*’ *aveyri* to *Triassologus*, further exemplifying similarities between South African and Australian Triassic insect faunas (Tierney *et al.* 2020; Béthoux & Anderson 2021).

Bechly (1997) considered that RP2 is branched in *Triassologus biseriatus*. However, bearing in mind the propensity of intercalary veins to acquire a main vein habitus points to Odonata in general and Triadophlebiomorpha in particular, an alternative option, favoured herein, is that the apparent anterior branch of RP2 (large blue arrow on Fig. 4B-D, F) instead is the first I- in the area between $I_{rp1-rp2}$ and RP2.

Triassologus biseriatus Riek, 1976
(Figs 4-6A)

Triassologus biseriatus Riek, 1976: 793, text-fig. 1, pl. 1, fig. 5. — Bechly 1997: 56.

Reisia rieki Deregnaucourt, Wappler, Anderson & Béthoux, 2017: 615, figs 1-2, n. syn.

EXAMINED MATERIAL. — Holotype, specimen BP/2/20948 (left wing in ventral aspect; Fig. 4A, B); and specimens PRE/F/5118 (Fig. 4D, E) and PRE/F/10125 (Fig. 5B, C) (all specimens, Anderson collection, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa).

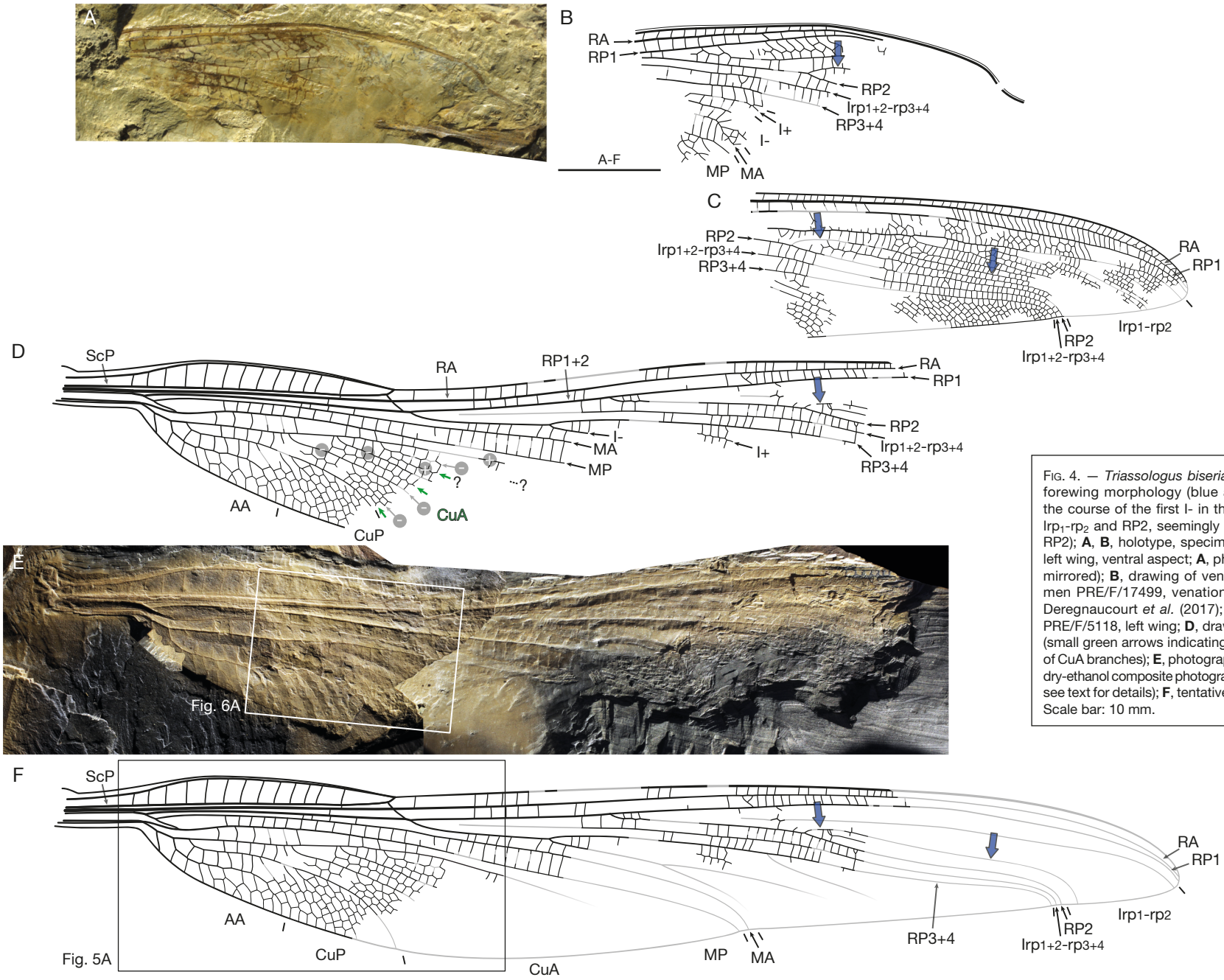


FIG. 4. — *Triassologus biseriatus* Riek, 1976, forewing morphology (blue arrows indicate the course of the first I- in the area between lrp1-rp2 and RP2); **A, B**, holotype, specimen BP/2/20948, left wing, ventral aspect; **A**, photograph (light-mirrored); **B**, drawing of venation; **C**, specimen PRE/F/17499, venation, redrawn from Deregnacourt *et al.* (2017); **D-F**, specimen PRE/F/5118, left wing; **D**, drawing of venation (small green arrows indicating the termination of CuA branches); **E**, photograph (patchwork of dry-ethanol composite photographs of each side; see text for details); **F**, tentative reconstruction. Scale bar: 10 mm.

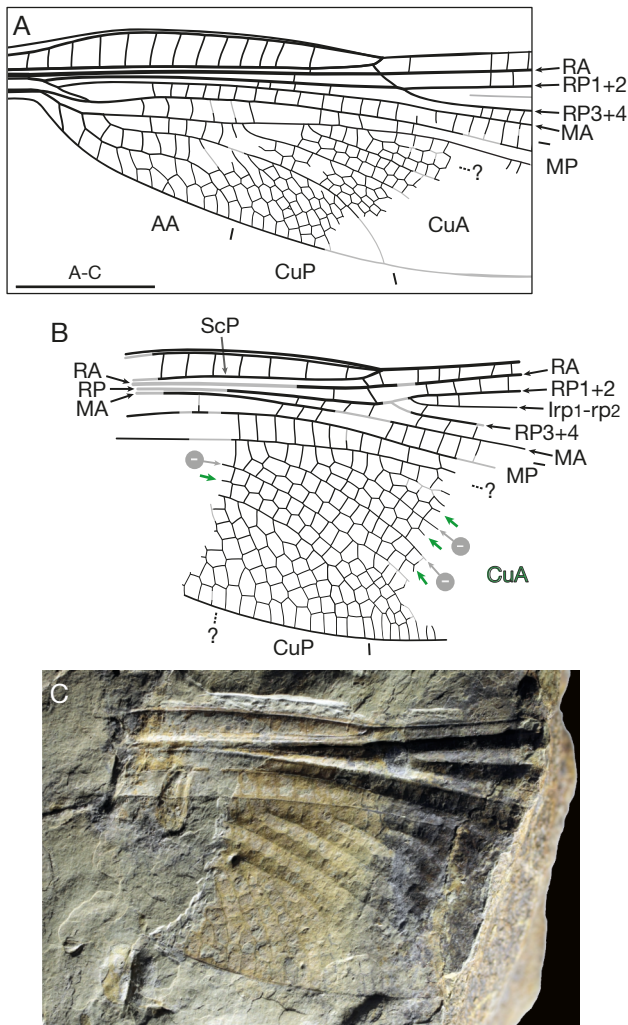


FIG. 5. — *Triassologus biseriatus* Riek, 1976: **A**, reconstruction of forewing morphology, location as shown on Fig. 4F; **B**, **C**, specimen PRE/F/10125a, left hindwing; **B**, drawing of venation (small green arrows indicating the termination of CuA branches); **C**, photograph (light-mirrored). Scale bar: 10 mm.

TYPE LOCALITY AND STRATIGRAPHY. — The holotype and the specimen PRE/F/10125 were found at the ‘Birds River’ locality (locality code Bir 111; see Anderson & Anderson 1984); material described by Deregnacourt *et al.* (2017), Kapokkraal and Aasvoëlberg localities (Kap 111 and Aas 411, respectively); and specimen PRE/F/5118, Hlatimbe Valley (Hla 213); all South Africa; Molteno Formation; lower Carnian, Upper Triassic (Anderson *et al.* 1998).

EMENDED DIAGNOSIS. — Maximum width about 17 mm in forewing and about 19.5 mm in hindwing (about 24 mm in *Triassologus avevri* n. comb., known from a putative forewing), forewing length about 110 mm.

SPECIMEN DESCRIPTIONS

Specimen PRE/F/5118 (Figs 4D, E, 6A)

Adpression preserving a left wing in dorsal (PRE/F/5118b; wing basal and median parts; extreme base, most of posterior area, and apical area missing) and ventral (PRE/F/5118a; about the first wing third, with portion of posterior wing margin missing opposite the pons) aspects; preserved length 84.5 mm, estimated total length about 110 mm; preserved maximum

width 13.6 mm, estimated total maximum width about 16.0 mm; petiole 3.5 mm wide; area between anterior wing margin broad (maximum width 2.9 mm); MA 1.0 mm long between its origin (from RP+MA) to its point of connection with the pons; distal to the pons and basal to the nodus, RA, RP and MA running very close to each other but distinct; nodus located 33.7 mm from wing base; nodal and sub-nodal cross-veins short, moderately strong, sub-aligned, oblique; RP1+2/RP3+4 fork located shortly after sub-nodal cross-vein; RP1+2 19.3 mm long; first I- between $I_{rp_1-rp_2}$ and RP2 seemingly emerging from RP2; first I- in the area between RP3+4 and MA originating 13.6 mm distal to the RP1+2/RP3+4 fork; pons oblique, 2.5 mm long; MP/Cu+AA fork opposite that of RP/MA; MP without obvious preserved branch; Cu+AA 2.8 mm long, Cu 1.6 mm long; in CuA-CuP area, the first 2 I- rectilinear and seemingly originating from CuA, the third I- originating as convex element shortly turning concave (possibly fused with a CuA branch at its origin); CuA branches zigzagging and seemingly originating from cross-venation; CuP and AA posteriorly pectinate; CuP curved, with 6 branches preserved (probably 7 in total), with intercalary veins between them; AA sigmoidal, with a maximum of 3 cells between it and the posterior wing margin; posterior wing margin forming a sharp angle opposite the RA/RP+MA fork.

Specimen PRE/F/10125 (Fig. 5B, C)

Adpression preserving a section of a left hindwing, opposite the nodus, in dorsal (PRE/F/10125b) and ventral (PRE/F/10125a) aspects; preserved length about 30.2 mm, maximum width (opposite nodus), 19.5 mm; area between anterior wing margin and ScP not particularly broad (maximum width 2.9 mm); basal to the nodus, RA, RP and MA poorly preserved, substantiated by smoothed depression (RP) and elevations (RA, MA); nodal and sub-nodal cross-veins short, moderately strong, sub-aligned, oblique; RP1+2/RP3+4 fork located shortly after sub-nodal cross-vein; $I_{rp_1+2-rp_3+4}$ seemingly diverging from RP1+2; in CuA-CuP area, I- rectilinear and CuA branches zigzagging; CuP reaching the posterior wing margin opposite the nodus.

REMARKS

The limited knowledge on triadophlebiomorphans available at the time coupled with the incompleteness and damaged condition of the holotype (Fig. 4A, B) made it virtually impossible for Riek (1976) to interpret its wing venation adequately. As a consequence, *Triassologus biseriatus* remained a rather mysterious Triassic species until Bechly (1997), based on data in the original description, proposed an alternative interpretation of the wing venation suggesting triadophlebiomorphaffinities. This proposal is herein corroborated. Comparison of the holotype with specimens assigned to ‘*Reisia*’ *rieki* (see Deregnacourt *et al.* 2017), and in particular the specimen PRE/F/17499 (Fig. 4C), and an hitherto undescribed forewing specimen (PRE/F/5118; Figs 4D, E, 6A), all from the same Formation, show that Riek’s ‘MA’ is actually $I_{rp_1+2-rp_3+4}$ (both veins are convex) and that the purported posterior

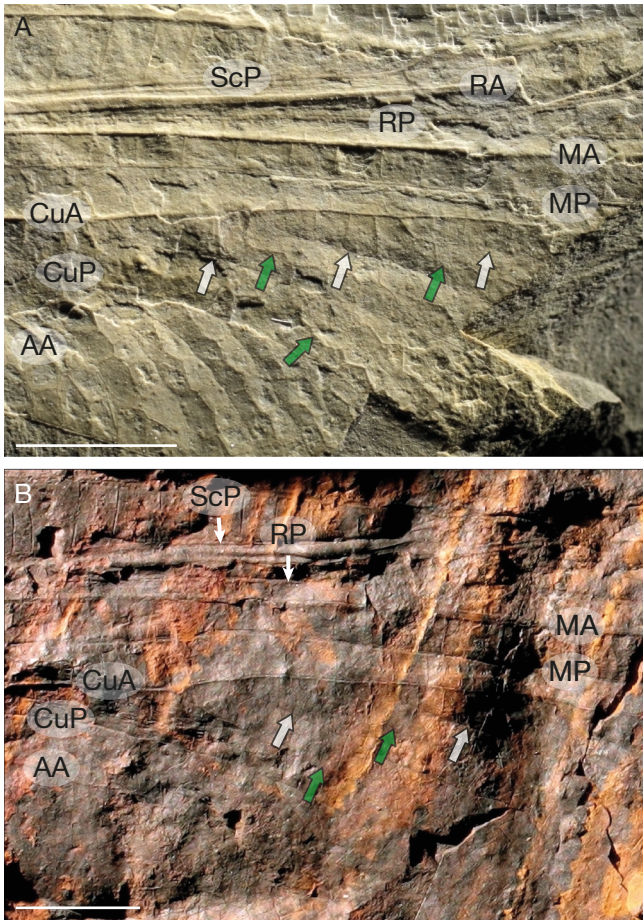


FIG. 6. — Detail of the organisation of CuA branches and of l - in the basal portion of the CuA-CuP area in *Triassologus* spp. (large green arrows, CuA branches; large white arrows, l cuA): **A**, *Triassologus biseriatus* Riek, 1976, specimen PRE/F/5118b (wing in dorsal aspect), flipped horizontally, location as shown on Fig. 4E; **B**, *Triassologus aveyri* (Béthoux & Beatie, 2010), n. comb., holotype, specimen AM F.132815. Scale bars: 5 mm.

branch of RP, apparently forked, is actually RP2 and its pseudo-fork. Further comparison between the holotype of *Triassologus biseriatus* and known material of '*Reisia*' *rieki* demonstrated that there are no substantial differences between them. Notably, wing sizes closely match, and the specimen PRE/F/16442 (see Deregnaucourt *et al.* 2017: fig. 1B) preserves the distinctive sigmoidal cross-veins occurring in the area between RP1 and l rp₁- l rp₂, opposite the RP2 pseudo-fork, conspicuous in the holotype. The species '*Reisia*' *rieki* must then be regarded as a junior synonym of *Triassologus biseriatus*.

The area preserved by the specimen PRE/F/5118 (Figs 4D, E, 6A) is largely unknown in other specimens. However, and luckily enough, it displays: i) a RP2 pseudo-fork; and ii) an area between the anterior margin and RA very narrow shortly after the RP2 pseudo-fork, both traits shared with other specimens preserving the corresponding area. An assignment of this specimen to *Triassologus biseriatus* is also corroborated by the wing morphology of *Triassologus aveyri* n. comb., which wing base is known and is largely consistent with that of the new specimen.

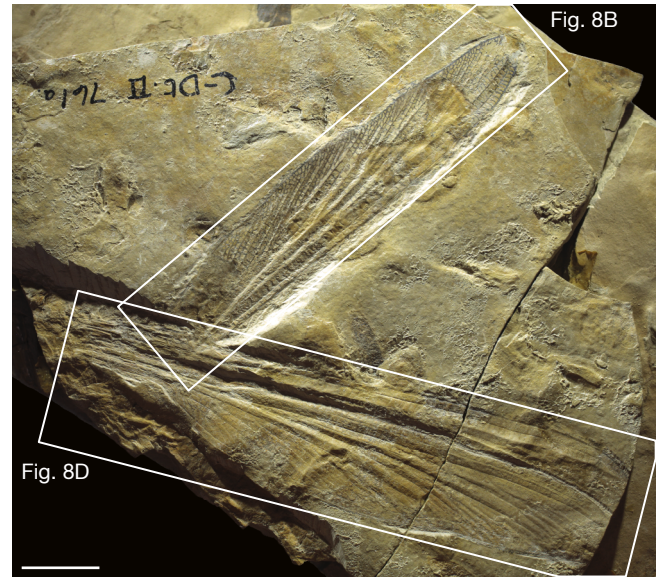


FIG. 7. — *Nototriadophlebia pritykinae* n. gen., n. sp., holotype, specimen BP/2/20950a (preserving the right forewing, isolated, in ventral aspect, and other wings, overlapping, in dorsal aspect), photograph (dry). Scale bar: 10 mm.

Finally, the specimen PRE/F/10125 (Fig. 5B, C) is regarded as a hindwing of *Triassologus biseriatus*. Indeed, every aspect of morphology conforms that of the forewing of the species (Fig. 5A), except for a more developed posterior area, and a slightly narrower area between the anterior wing margin and ScP. Both differences are common between fore- and hindwings of anisopterous Odonata, such as Anisoptera (see Garrison *et al.* 2006; among others). Incidentally, this record then suggests, for the first time, that some Triadophlebiomorpha were indeed anisopterous.

Genus *Nototriadophlebia* n. gen.

urn:lsid:zoobank.org:act:B255DC70-C175-4E48-BCAB-BFFCBEEBDC0D

TYPE SPECIES. — *Nototriadophlebia pritykinae* n. sp.; monotypic genus.

ETYMOLOGY. — The genus name derives from *Triadophlebia*, a related genus, to which was appended the prefix 'Noto' ('south' in Ancient Greek), referring to the geographic occurrence of its type species.

DIAGNOSIS. — As for the type species.

Nototriadophlebia pritykinae n. gen., n. sp. (Figs 7-9)

urn:lsid:zoobank.org:act:BB1717F8-0D90-41B5-9D88-68689FB9B410

HOLOTYPE. — Specimen BP/2/20950ab, adpression preserving four wings (Anderson collection, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; Figs 7, 8).

PARATYPE. — Specimen BP/2/20986ab, adpression preserving a single wing (Anderson collection, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; Fig. 9).

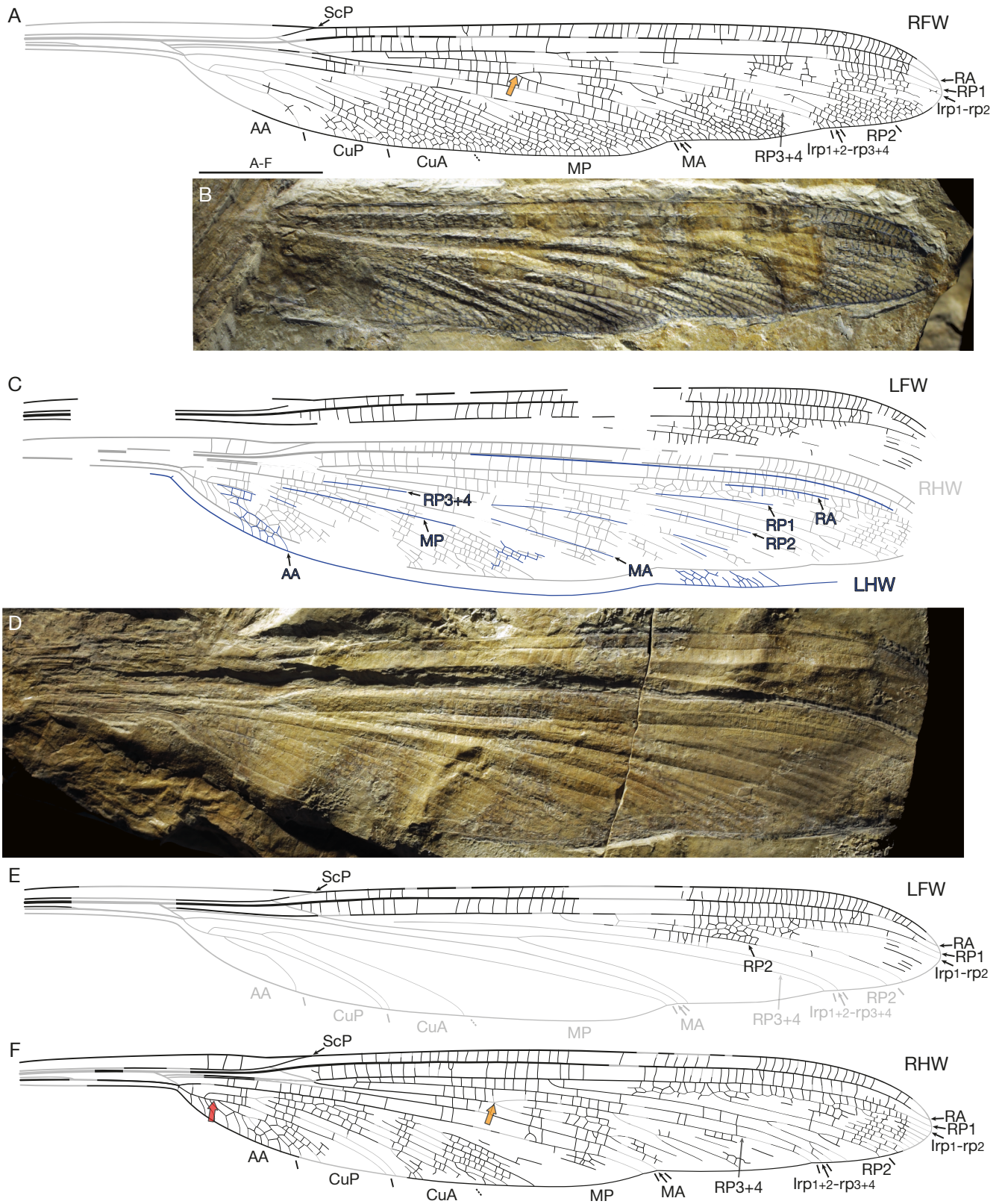


FIG. 8. — *Nototriadophlebia pritykinae* n. gen., n. sp., holotype, specimen BP/2/20950a: **A, B**, right forewing (RFW); **A**, drawing of venation, with tentative reconstruction of wing base; **B**, photograph, location as shown on Fig. 7 (dry-ethanol composite, light-mirrored, flipped horizontally); **C, D**, overlapping left forewing (LFW), right hind wing (RHW) and left hind wing (LHW; in blue); **C**, drawing of venation; **D**, photograph, location as shown on Fig. 7 (dry-ethanol composite, fragments readjusted digitally); **E**, left forewing (LFW), drawing of venation isolated from **C**, with tentative reconstruction of the posterior area; **F**, right hind wing (RHW), drawing of venation isolated from **C** (large red arrow, CuP+AA stem). Scale bar: 10 mm.

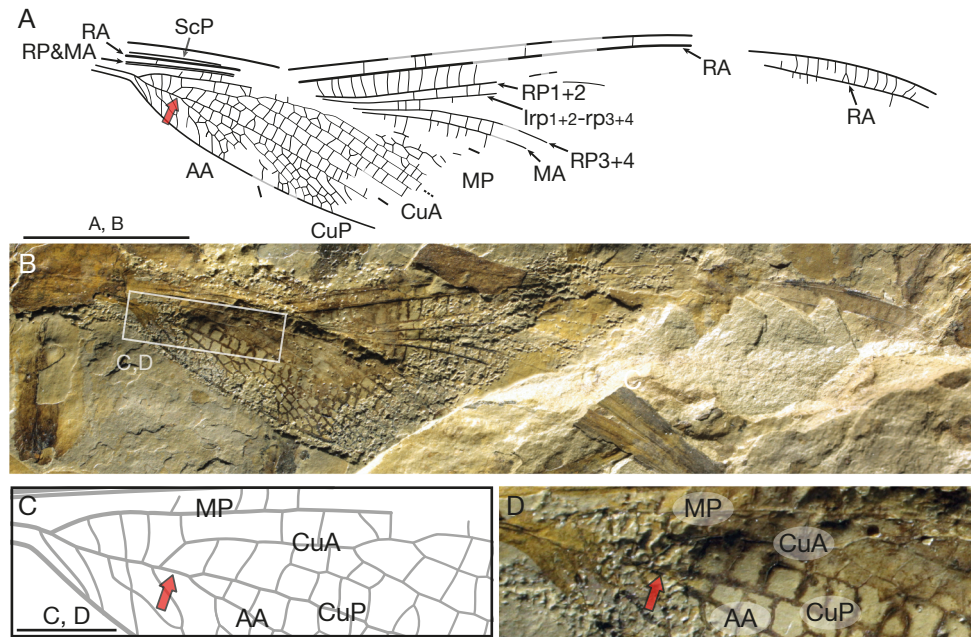


FIG. 9. — *Nototriadophlebia pritykinae* n. gen., n. sp., paratype specimen, BP/2/20986b, left wing (large red arrows indicating the CuP+AA stem): **A, B**, overview; **A**, drawing of venation; **B**, photograph (light-mirrored); **C, D**, detail of cubito-anal area, location as indicated on **B** (large red arrows, CuP+AA stem); **C**, drawing of venation; **D**, photograph (light-mirrored). Scale bars: A, B, 10 mm; C, D, 2 mm.

DIAGNOSIS. — Area between the anterior wing margin and RA (distal to the nodus) widening gradually to $\frac{4}{5}$ of wing length, where it is as wide as the RA-RP1 area (most prominent in forewing); first I- in the RP3+4-MA area (i.e. RP3+4 pseudo-fork; large orange arrows on Fig. 8A, F) arising before RP3+4 mid-length; CuP+AA stem splitting into CuA and CuP+AA (as opposed to Cu and AA; large red arrow on Figs 8F, 9A, C, D); AA reaching the posterior wing margin basal to the end of ScP; between the endings of MA and AA, posterior wing margin comparatively straight.

ETYMOLOGY. — The species epithet honours Lyudmila N. Pritykina, for her contribution to our knowledge of fossil Odonata, and of Triadophlebiomorpha in particular.

TYPE LOCALITY AND STRATIGRAPHY. — Both holotype and paratype were collected at Birds River (locality code 'Bir 111'; see Anderson & Anderson 1984), South Africa; Molteno Formation; lower Carnian, Upper Triassic (Anderson *et al.* 1998).

GENERAL DESCRIPTION

Fore- and hindwings subequal, very elongated, broadest at mid-length; wing length about 74 mm (as derived from holotype specimen; possibly down to 70 mm), maximum width about 11.0 mm (possibly down to 10.2 mm), width opposite nodus 7.1–7.6 mm); petiole long (about 12.8 mm) and narrow (width about 2.4 mm); ScP reaching the anterior wing margin basal to the first third of wing length; distal to the nodus, area between anterior wing margin and RA broadening gradually, at its broadest opposite the end of $Irp_{1+2}-rp_{3+4}$; structure of the nodus and origin of RP+MA, RP and MA unknown; RP1/RP2 fork in a position more distal than that of the point of origin of the first I- in the RP3+4 area; Irp_1-rp_2 weakly differentiated, zigzagging along RP1; occurrence of 3 I- (and I+ between them) forming RP2 posterior pseudo-branches in the distal part of the area between RP2 and $Irp_{1+2}-rp_{3+4}$; RP3+4

with a marked angle opposite the origin of the first I- (between RP3+4 and MA; large orange arrows on Fig. 8A, F); the two first I- in the area between RP3+4 and MA branched; in this area, total of about 8 I- reaching the posterior wing margin; MA simple, rectilinear, very close to RP3+4 in its basal third; marked inflexion of the posterior wing margin opposite the ending of MA; MP originating from MP+Cu+AA with a slight obliquity; branches of MP and CuA not clearly distinguishable (probable occurrence of a CuAprlg), CuA with 2 branches at least, and with a I- distally branched between its two (first posterior) branches; MP and CuA covering more than a quarter (less than a third) of the posterior wing margin length; Cu+AA splitting into CuA and CuP+AA, CuA diverging very obliquely; CuP rectilinear, with about 4–5 posterior branches and I+ between them; AA gently curved, reaching the posterior wing margin basal to the end of ScP.

SPECIMEN DESCRIPTIONS

Specimen BP/2/20950 (Figs 7; 8)

Adpression preserving four wings, with side BP/2/20950a preserving the right forewing (isolated) and left wings in ventral aspect, and right hindwing in dorsal aspect (the three latter largely overlapping); and its reverse side BP/2/20950b.

Right forewing (Figs 7; 8A, B). Well preserved, with area basal to the nodus and small portion of apex missing; preserved length 55.6 mm, maximum width 10.7 mm, width opposite nodus about 7.6 mm.

Left forewing (Figs 7; 8C–E). Only anterior-most area decipherable; preserved length 73.2 mm; estimated total length about 74.2 mm.

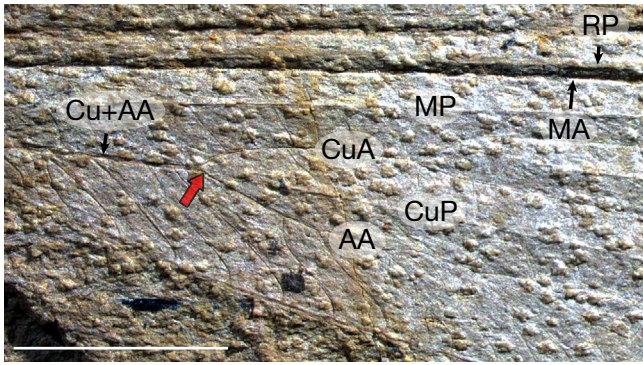


FIG. 10. — Detail of the cubito-anal area in *Neritophlebia longa* Pritykina, 1981, holotype, specimen PIN 2555/614, left wing (large red arrow, CuP+AA stem). Scale bar: 4 mm. Courtesy A. S. Felker.

Right hindwing (Figs 7; 8C, D, F). Well preserved, with nodal area and part of apex missing, and venation in the petiole difficult to decipher; basal to the nodus, RP and MA not distinguishable from each other (assumed to closely overlap); cubito-anal area preserved, showing a CuP+AA stem.

Left hindwing (Figs 7; 8C, D). Barely decipherable but for the posterior wing margin, with a sharp inflexion opposite the end of MA.

Specimen BP/2/20986 (Fig. 9)

Adpression preserving a left wing in ventral (BP/2/20986b) and dorsal (BP/2/20986a) aspects, largely incomplete and creased/disrupted opposite the nodus and, roughly, opposite the termination of MA; preserved length about 51 mm; width opposite the nodus (assuming the wing is creased at the nodus) about 7.1 mm; RP and MA not distinguishable (assumed to closely overlap); Cu+AA splitting into CuA and CuP+AA; AA reaching the posterior wing margin basally.

REMARKS

A prominent character state displayed by the specimen BP/2/20950 is the splitting of the Cu+AA stem into CuA and CuP+AA (instead of Cu and AA; red arrows on Figs 8F; and see Fig. 9A, C, D). Within Triadophlebiomorpha, this trait is present only in some representatives of the super-family Triadophlebioidea (see Pritykina 1981; Zheng *et al.* 2017b: fig. 3C; Fig. 10) and may have an unforeseen relevance to delimit a subset within this group. However, provided that: i) severe deformation endured by Madygen material, representing most of the corresponding specimens, may have not been fully taken into consideration for species delimitation; and that ii) the character state may have been subjected to intra-specific variation in some species, we refrained from erecting a new taxon name for this subset. Yet, comparison with those taxa displaying a CuP+AA stem (as least in some of the known species) is a legitimate first step.

Further compared to most of these taxa, the specimen is distinctive in the shape of the area between the anterior wing margin and RA (distal to the nodus), gradually broadening

until the $\frac{4}{5}$ of wing length (‘pterostigmatic area’), where it is as wide as the RA-RP1 area. This trait is shared with *Mitophlebia* Pritykina, 1981, *Sinotriadophlebia* Zheng, Nel & Zhang in Zheng *et al.* (2017a), and, possibly, *Neritophlebia* Pritykina, 1981 (considering that the first and last genera are known from heavily deformed material). Affinities with *Mitophlebia* can be excluded owing to the higher development of the RP3+4 area in the new specimen. In *Neritophlebia* the RP1+2/RP3+4 fork is located well distal to the nodus (or, ending of ScP), but is in a more basal position in the new specimen. Similarly, AA reaches the posterior wing margin more basally. Finally, the new specimen can be distinguished from *Sinotriadophlebia* owing to the shape of the posterior wing margin between the endings of MA and AA, with a median section straighter in the new specimen; and, likewise, a more basal ending of AA. Moreover, *Sinotriadophlebia* has the RP1/RP2 fork located basal to the point of origin of the first I- in the RP3+4 area, while it is the opposite in the new specimen (and all other Triadophlebioidea). Observed differences between the new material and known Triadophlebioidea legitimate the erection of a new species and genus.

At a time when the Triadophlebiomorpha were yet poorly known, the paratype specimen (also bearing the collecting number ‘C-Dt. II 758’) was regarded by Riek (1976) as possibly belonging to *Triassoneura heidiae* Riek, 1976. This is excluded, in the first place due to the lack of a pterostigma, which would have been visible in the preserved portions. Moreover, it clearly displays a CuP+AA stem (emerging from Cu+AA; large red arrow on Fig. 9A, C, D), a broadening of the distal part of area between the anterior wing margin and RA, a comparatively basal ending of AA, all features congruent with an assignment to the same Triadophlebioidea species as the specimen BP/2/20950. As far as it can be appreciated, it is only slightly smaller than it.

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