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Authors: Béthoux, O., and Nel, A.

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# New data on Tcholmanvissiidae (Orthoptera; Permian)

O. Béthoux and A. Nel

(OB, AN) Laboratoire d'Entomologie and UMR 8569, Muséum National d'Histoire Naturelle, 45 rue Buffon, F-75005 Paris, France. E-mail: anel@mnhn.fr
(OB) UMR Botanique et Bioinformatique de l'Architecture des Plantes, UMR 5120, 2196 Bd. de La Lironde, TA40/PS2, F-34398 Montpellier France. E-mail: bethoux@cirad.fr

## Abstract

The composition and members of the Tcholmanvissiinae (representatives of the 'oedischioids' stem-group) are revised. One of us (O.B.) examined all available specimens, allowing a better appreciation of intraspecific variability in the wing venation and a proposal of new diagnostic specific and generic characters. Several genera and species are synonymized. Finally, close relationships between Tcholmanvissiinae and Tettoedischiinae are supported by data on relief of veins and organization of the cubital area. Previous hypotheses of relationships between Tcholmanvissiinae and Titanoptera or Caelifera are dismissed.

## Key words

Orthoptera, Permian, fossil, Tcholmanvissiinae, Tettoedischiinae, 'oedischioids', forewing venation pattern

## Introduction

Because the Ensifera and Panelcanida (including Caelifera) have both derived from the extinct 'oedischioids' (Béthoux & Nel 2002), the resolution of the relationships within this potential stem group is of crucial importance in order to define the proper sister groups of these large clades. The phylogenetic attempt by Sharov (1968, translated to English in 1971), proposing a sister-group relationship between Caelifera and Tcholmanvissiidae, was dismissed by Gorochov (1996), who supported instead a sister-group relationship between Caelifera and Xenopteroidea. Béthoux & Nel (2002) also dismissed Gorochov's hypothesis, and proposed that the Caelifera are related to Elcanidae, and concluded that the characters currently available are not sufficient for a reliable phylogenetic reconstruction of the most basal 'oedischioids'.

The 'tcholmanvissiids' are 'keystone' taxa for the phylogeny of the 'oedischioids'. Sharov (1968) expected close relationships between them and Caelifera, Titanoptera and Phasmatodea. Gorochov (1995a, 1995b) proposed to include the 'Tcholmanvissiinae' (as a subfamily) within a paraphyletic family Oedichiidae, 'primitive' in respect to all Orthoptera except Elcanoidea + Permoraphidioidea (see also Gorochov & Rasnitsyn 2002 for placement of 'oedischioids' within Orthoptera). One of us (O.B.) made new observations during a trip to Moscow in April 2002, which justify the present review of the 'tcholmanvissiid' material.

## Materials and Methods

The venation patterns and vein widths were drawn, using a stereo-microscope and a camera lucida, directly from the fossil surface, dry and under alcohol. Both part and counterpart were examined, when available. Thus, in some instances, drawings show information not visible on photographs of fossils. Because of their size (our original drawing of *Tcholmanvissiella gigantea* measured 60 cm long), original drawings suffered distortion from base to tip. Thus, they were readjusted on photographs using image-editing software.

Because of the length of several fossils, in order to have optimal resolution of digital photographs, views from basal and distal halves were taken separately and joined together using image-editing software. When possible, counterparts were light-mirrored in order to show the relief as viewed from dorsal side.

We follow the nomenclature of Béthoux & Nel (2001, 2002) proposed for the ground plan of the 'panorthopteroid' insects: ScP, Subcosta Posterior; R, Radius; RA, Radius Anterior; RP, Radius Posterior; M, Media; MA, Media Anterior; MP, Media Posterior; CuA, Cubitus Anterior; CuP, Cubitus Posterior; CuPa, anterior branch of CuP; CuPaα, anterior branch of CuPa; CuPaβ, posterior branch of CuPa; CuPb, posterior branch of CuP; AA1: first Analis Anterior; AA2: second Analis Anterior.

## Systematic Paleontology

In the present work, only the better-preserved specimens are fully described. Differences and additional information are noted for other specimens. All fossils are stored in the collections of the Palaeontological Institute of the Russian Academy of Science (PIN), Moscow. The origins of the specimens are established after the first number, which designate the collection number. The correspondences between collection numbers and deposits are available on http://palaeoentomolog.ru/Collections/rus_loc.html.

### *Tcholmanvissiidae* Zalessky 1934 *sensu nov.*

*Diagnosis.*— CuPaα with at least one branch basal or at its connection with CuA.

*Composition.*— This family comprises the 2 subfamilies Tcholmanvissiinae Zalessky 1929 and Tettoedischiinae Gorochov 1987 (genera *Macroedischia* Sharov 1968 and *Tettoedischia* Sharov 1968; subfamily previously included in Oedischiidae, see Gorochov 1995a).

*Remark on taxa ranking.*— The familial and subfamilial taxonomic conclusions reached by Gorochov (1995a, 1995b) about the superfamily Oedischioidea Handlirsch 1906, are problematic: the composition and the monophyly of the subfamily Oedichiinae Handlirsch 1906 are debatable; the monophyly of the subfamilies Elcanoedischiinae Gorochov 1987, Pruvostitinae Zalessky 1929 and Sylvoedischiinae Gorochov 1987 remains to be demonstrated; and the Pruvostitidae Zalessky 1929 could be paraphyletic in respect to the 'Oedichiidae' (excluding *Oedischia* Brongniart 1885, type-species of the family) (Béthoux *et al.* 2002, Béthoux & Nel 2002). Because the 'apomorphies' of the family Oedischiidae (including Tcholmanvissiinae and Tettoedischiinae among other taxa) proposed by Gorochov (1995a, 1995b) are not supported by cladistic analysis (Béthoux & Nel 2002), we propose a revised taxonomy.

The close relationship of Tcholmanvissiinae with Tettoedischiinae proposed by Gorochov (1995b) is supported by this study (see below). Thus, we propose to use the Tcholmanvissiidae in a new sense, including the taxa assigned by Sharov (1968) to Tcholmanvissiidae plus *Macroedischia* and *Tettoedischia*. It is identical to the clade considered by Gorochov (1995a, 1995b) as (Tcholmanvissiinae + Tettoedischiinae).

*Remark on family composition.*—*Tettoedischia minuta* Sharov 1968, undoubtedly closely related to *Macroedischia* within Tettoedischiinae, has a free and simple CuPa$\alpha$, without any clear anterior branch reaching CuA (see Sharov 1968, Fig. 8.D, with 'CuA2' = CuPa$\alpha$, 'MP + CuA1' = CuA + CuPa$\alpha$; O.B., pers. obs.), *contra* supra-ordinal diagnosis. Nevertheless it has the organization of 'tcholmanvissids' with a distinct branch of CuPa$\alpha$ reaching the posterior wing margin without any fusion with CuA. This absence of fusion between CuA and a branch of CuPa$\alpha$ is rare within the Panorthoptera (Béthoux & Nel 2002). *T. minuta* is based on a single forewing that could have an aberrant venation. Thus, as it is very close to *Macroedischia*, we provisionally consider that its cubital pattern is compatible with the familial diagnosis.

Lin (1987), followed by Gorochov (1996a), included the genus *Yinpingia* Lin 1987 in 'tcholmanvissiids' (-iidae for the former author, -iinae for the latter). Study of an original photograph of the fossil (provided by Dr. Huang Diying, Nanjing Institute of Geology and Paleontology, Academia Sinica, PR China) revealed that *Yinpingia* does not share the diagnostic additional branch of CuPa$\alpha$ before connection with CuA, but has the classical medio-cubital pattern of Orthoptera (Béthoux & Nel 2001, 2002). Thus, we exclude it from the Tcholmanvissiidae. Furthermore, the absence of a connection of MA/MA1 with RP in *Yinpingia* is widespread in 'oedischioids' and cannot alone support its inclusion in Tcholmanvissiinae.

### *Tcholmanvissiinae* Zalessky 1934

*Diagnosis.*— Forewings. Area between RA and RP broadened (about 1/4 of wing width at best; about 1/5 in Tettoedischiinae); absence of connection of an anterior branch of MA with RP; point of separation between MA and MP very close (< 3 cells) to origin of distal (free) part of CuA.

*Composition.*— Type-genus: *Tcholmanvissia* Zalessky 1929.
Other genera: *Jubilaeus* Sharov 1968, *Tcholmanvissiella* Gorochov 1987.

*Discussion.*—The Tcholmanvissiinae can be distinguished from the Tettoedischiinae by the above diagnostic characters but also by the absence of a connection between the most anterior branch of RA with ScP. Nevertheless, this character is present in others representative of the 'oedischioids', and its polarization must be confirmed.

The character 'absence of a connection of an anterior branch of MA with RP' is also present in other representatives of the 'oedischioids' (Gorochov 1996a). In any case, it is clearly apomorphic within the family Tcholmanvissiidae.

### *Tcholmanvissia* Zalessky 1929

*Tcholmanvissia* – Zalessky 1929, p. 19-21, Fig. 8 (original description).
*Tcholmanvissia* – Zalessky 1934, p. 154-155, Fig. 3 (additional material assigned to a new species *T. explicator*).
*Metoedischia* (in part) – Martynov 1940, p. 34-36 + 58-59, Fig. 36 (additional material assigned to a new species *M. longipes*).
*Pinegia* (in part) – Sharov 1962, p. 148, Fig. 390 (generic synonymy, description of additional material of *M. longipes*).

*Diagnosis.*—Forewing: Area between RA and RP broadened; area between veins MA and MP broadened (broader than area between MP and anterior stem of CuA + CuPa$\alpha$), with strongly sigmoidal cross-veins in basal half; veins CuPb, CuPa$\beta$ and posterior branch(es) of CuPa$\alpha$ simple. The branching pattern of CuPa$\alpha$ before its connection with CuA is variable. As the variability is unknown in other genera of the subfamily, this character may be diagnostic for several genera or the whole subfamily Tcholmanvissiinae.

*Discussion on previous proposals of generic synonymy.*— Sharov (1962: 148 – translated in 1991:192 –; 1968: 28 – translated in 1971: 27) proposed to synonymize *Tcholmanvissia* Zalessky 1929 with *Pinegia* Martynov 1928 (original description at p. 47). The type species of *Tcholmanvissia*, *Tcholmanvissia noinskii* Zalessky 1929, is based on a fragment of the forewing base (see Zalessky M. D. 1932: text.-Fig. 3, pl. XIII Fig. 3; see Zalessky G. M. 1934 for in-text emendation of original drawing). The type species of *Pinegia*, *Pinegia oknowae* Martynov 1928, is based on the apical part of a hind wing. These two fossil wings have no part in common available for comparison. Sharov (1968) based his synonymy on further isolated fore and hind wings that he attributed to *Pinegia longipes* (Martynov 1940). Unfortunately, the type specimen of *P. oknowae* has no particular diagnostic character that would be uniquely shared by the other more complete hind wings described by Sharov. Sharov (1968) distinguished the hind wing of *Pinegia* (based on the study of *P. longipes*), relative to *Jubilaeus beybienkoi* Sharov 1968 by "the bifurcation of MA … further displaced towards the apex and … situated at the level of the beginning of the branching of RS". But in the original drawing of *P. oknowae*, the fork of MA is clearly in a very basal position, much more basal than the first branch of RP. Also, *P. oknowae* has 6 to 7 free anterior branches of RA, unlike *P. longipes*. Thus, we consider the genus and species *P. oknowae* as an Orthoptera *incertae sedis*, and here remove it from synonymy under *Tcholmanvissia*.

*Tcholmanvissia* was also considered as a junior synonym of *Thnetodes* Martynov 1928 (Sharov 1962, 1968; Carpenter 1992). Unfortunately, the type specimen of *Thnetodes craticius* Martynov 1928 (type species) is only a fragment of a wing with no diagnostic character. Sharov and Carpenter also considered *Kamaites* Zalessky 1929 (type species *Kamaites mirabilis* Zalessky 1929) and *Tylliardiella* Martynov 1930 (type species *Tylliardiella distincta* Martynov 1930) as junior synonyms of *Pinegia*. Both are also very poor and fragmentary fossils. We follow Gorochov (1995a: 76) who considered all these taxa as *incertae sedis*. In conclusion, we restore *Tcholmanvissia* Zalessky 1929 as a valid genus.

*Composition.*— Type-species *Tcholmanvissia noinskii* Zalessky 1929 (Early Kazanian, Late Permian; Tikhie Gory beds, Tatarstan, Russia; Iva-Gora beds, Arkhangelsk region, Russia); *Tcholmanvissia longipes* (Martynov 1940) *comb. nov.* (Late Kungurian, Early Permian; Tshekarda, Russia).

Despite the fact that *T. noinskii* is the type species, we first revise *T. longipes* because its available set of specimens is more complete than for the type specimen of *T. noinskii*.

### *Tcholmanvissia longipes* (Martynov 1940) *comb. nov.*

Figs 1-5

*Metoedischia longipes* – Martynov 1940, p. 35, Fig. 36 (original description).
*Pinegia longipes* – Sharov 1962, p. 148, Fig. 390 (generic synonymization and description of additional material).
*Pinegia longipes* – Sharov 1968, p. 31, Fig. 12 (description of additional material).
*Pinegia longipes* – Carpenter 1992, p. 158, Fig. 97.1 (citation).
*Pinegia longipes* – Gorochov 1995, Figs 154-158 (figuration).

*Material.*—Type specimen PIN 34/118; other examined material: specimens PIN 1700/1488, PIN 1452/5, PIN 1700/1531, PIN 1700/1454 and PIN 1700/1483, housed in the Palaeontological Institute, Russian Academy of Sciences (Moscow).

*Diagnosis.*—Forewing distinctly narrower than *T. noinskii* (width not exceeding 11 mm instead of 15 mm in *T. noinskii*); also branching of CuPa into CuPa$\alpha$ and CuPa$\beta$ opposite distal end of ScA on anterior margin.

Note: '*Pinegia*' *longipes* was originally attributed to the genus *Metoedischia*, but *Metoedischia magnifica* Martynov 1928, type species of this latter genus, does not have the additionally basal branch of CuPa$\alpha$ proper to the Tcholmanvissiidae and clearly present in the type specimen of '*Pinegia*' *longipes*. Thus, its exclusion from *Metoedischia* is well supported. There are few differences between the comparable structures in *T. noinskii* and '*Pinegia*' *longipes* (structures of the fore wing base), *viz.* the size and the presence of two branches of CuPa$\alpha$ basal of its connection with CuA. This last character is quite variable among the available material of Tcholmanvissiinae (see below). Both do not support a generic separation. Thus, we propose to attribute '*Metoedischia*' ('*Pinegia*') *longipes* to the genus *Tcholmanvissia*.

*Redescriptions.*— The type specimen is fragmentary but shows the main diagnostic characters of the genus and species, which are also visible in the other specimens attributed to this species.

Specimen PIN 1700/1488 (Fig. 1): Part and counterpart of a fragment of body with 3 wings, 2 wings superimposed and the isolated, almost complete, right forewing; the following description only concerns this last wing.

Wing length about 63.7 mm, width 10.8 mm; posterior wing margin with a strong inflexion opposite first branching of RP; shape of basal part of 'precostal' area not well distinguished; ScA sigmoidal, ending on anterior margin about 16.7 mm distal of wing base; ScP long, reaching anterior wing margin about 56.3 mm distal of wing base; cross-veins between ScA and ScP straight and simple, regularly spaced, without cross-veins between them; R strongly marked, basally distinct from M + CuA, slightly posteriorly bowed opposite origin of CuA from M + CuA; base of RP 35.6 mm distal of wing base; RA anteriorly pectinate, with 6 simple branches; 3 basal branches of RA fused with ScP; cross-veins between ScP and R/RA straight (in basal part) to sigmoidal (in distal part); RP posteriorly pectinate, with 5 main branches reaching wing apex and a total of 7 branches reaching margin; first and fourth branches of RP distally forked; area between RA and RP strongly broadened in its basal quarter (max. width 2.7 mm), progressively narrowing in distal 3/4; cross-veins in broader part of area between RA and RP hardly distinguishable; course of CuA well discernable: M + CuA, free CuA and CuA + CuPa$\alpha$ more marked than other veins of medio-cubital area and distinctly convex; origin of CuA from M + CuA about 19.0 mm distal of wing base; M very short (1.1 mm) before origin of MA; MA branched very distally, opposite max. width of area between RA and RP; MA not regularly branched, with 5 branches reaching posterior wing margin; cross-veins between branches of RP, MA and MP hardly discernable in distal third of wing (probably reticulated); MP distinctly concave, branched roughly opposite basal branch of MA, with only 2 branches reaching posterior wing margin; area between MA and MP basally slightly broadened, with strongly sigmoidal cross-veins, progressively straightened; CuA moderately long (1.8 mm) before connection with CuPa$\alpha$; CuA + CuPa$\alpha$ posteriorly pectinate, with 4 simple branches; additional posterior branch of CuPa$\alpha$ opposite connection between CuA and CuPa$\alpha$; CuP and AA1 very approximate (common stem?) at their visible origins; CuP branched very basally; long CuPa before its separation as CuPa$\alpha$ and CuPa$\beta$, which is opposite estimated end of ScA on anterior wing margin; CuPa$\alpha$ branched opposite its connection with CuA, 5.9 mm distal of its origin; posterior branch of CuPa$\alpha$, CuPa$\beta$, CuPb, AA1 simple (also AA2 in its preserved part); cross-veins in distal parts of areas between branches of CuA + CuPa$\alpha$, posterior branch of CuPa$\alpha$, CuPa$\beta$ and CuPb, sigmoidal, subparallel to posterior margin; AA3 posteriorly branched.

Specimen PIN 1452/5 (Fig. 2): Part and counterpart of an incomplete right forewing (posterior margin and distal third missing); anterior wing margin not discernable before end of ScA; cross-veins in area between anterior wing margin and ScP basally straight to distally sigmoidal, all simple and without reticulation; cross-veins in area between RA and RP bowed towards apex, most of them simple, not reticulated in preserved part; cross-veins in basal part of area between MA and MP not reticulated and sigmoidal, most of them simple; CuPa branched into CuPa$\alpha$ and CuPa$\beta$ opposite estimated end of ScA on anterior margin; CuPa$\alpha$ with 2 free posterior branches before its fusion with CuA; CuA + CuPa$\alpha$ with at least 5 branches.

Specimen PIN 1700/1531 (Fig. 3): Counterpart of a very incomplete right forewing, with wing margins, distal two thirds and anal area missing; ScA anteriorly pectinate; origin of CuPa$\alpha$ and CuPa$\beta$ 11.1 mm distal of origin of CuPa; origin of basal branching of CuPa$\alpha$ 1.32 mm distal of origin of CuPa$\alpha$; one additional fork of anterior branch of CuPa$\alpha$ opposite its connection with CuA.

Specimen PIN 1700/1454 (Fig. 4): Part and counterpart of the distal half of a right forewing; RP with 6 branches covering apex; areas between branches of RP, MA and anterior branch of MP with zigzagged convex secondary longitudinal veins parallel to main veins.

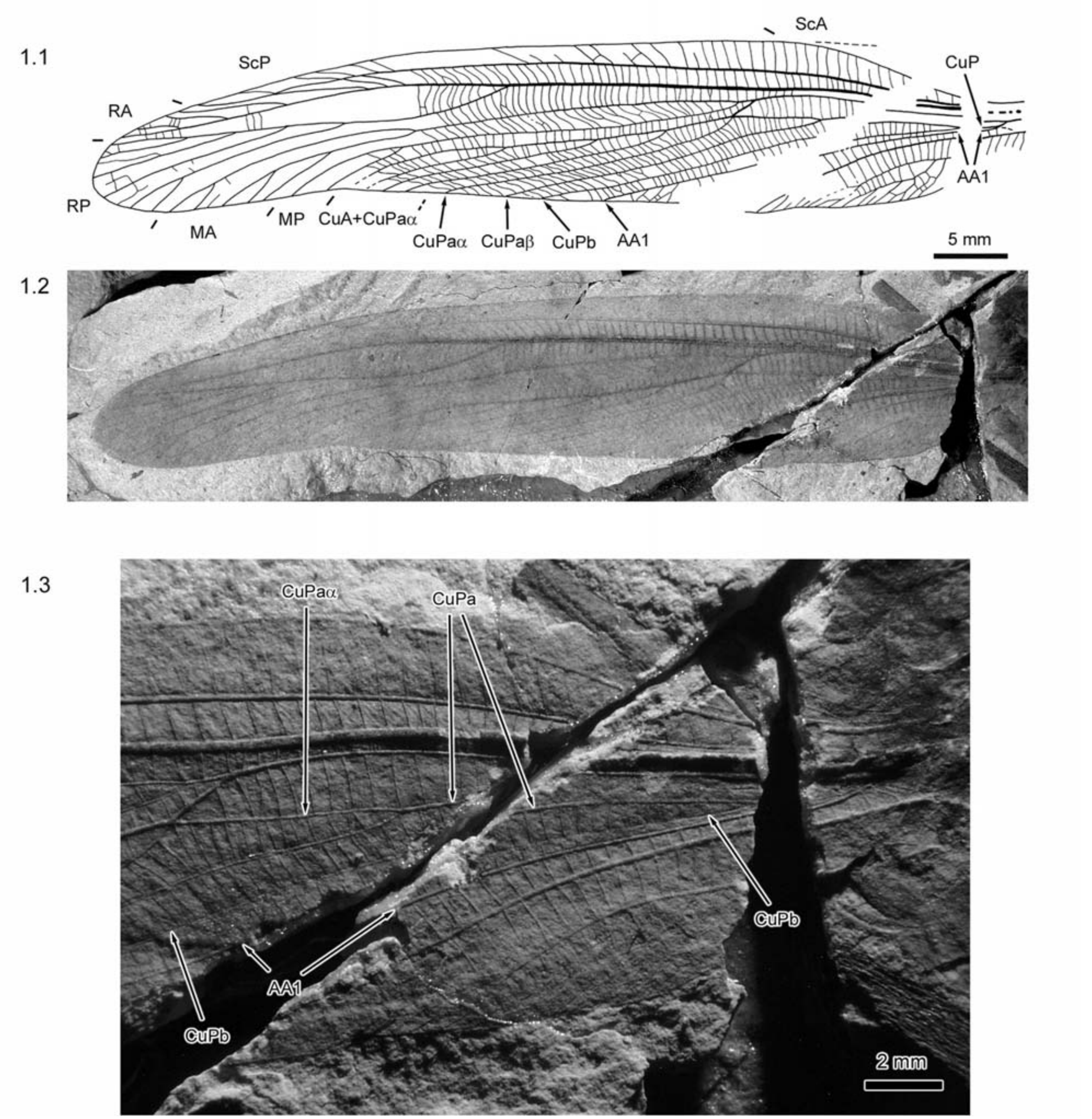


**Fig. 1.** *Tcholmanvissia longipes*, specimen PIN 1700/1488 (part and counterpart).
1.1 : reconstruction of the left forewing.
1.2 : photography of the left forewing (part).
1.3 : detailed photography of the basal third of the left forewing (part; low-angled light).

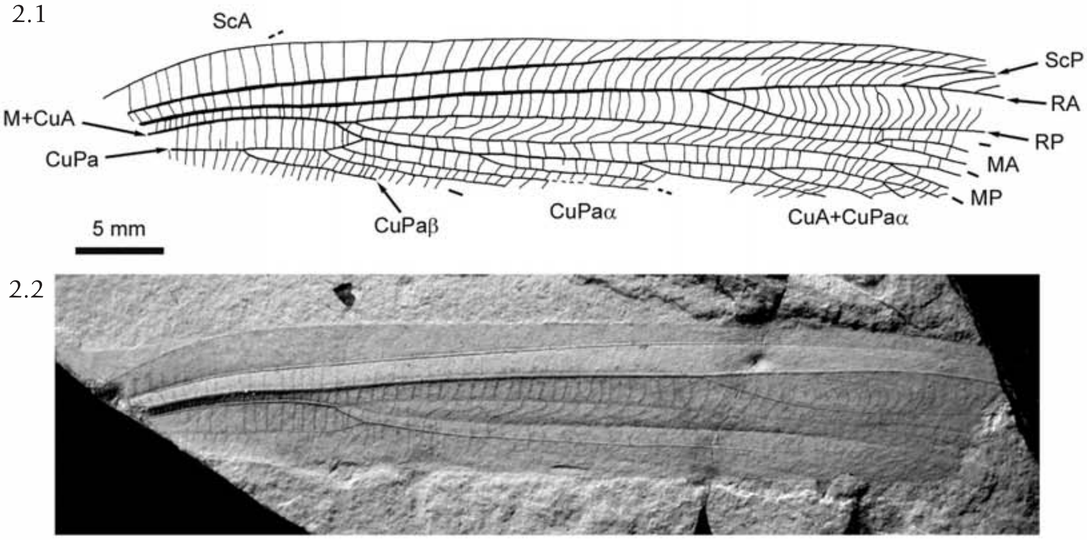


**Fig. 2.** *Tcholmanvissia longipes*, specimen PIN 1452/5 (part and counterpart).

2.1: reconstruction of the right forewing.

2.2: photography of the right forewing (part).

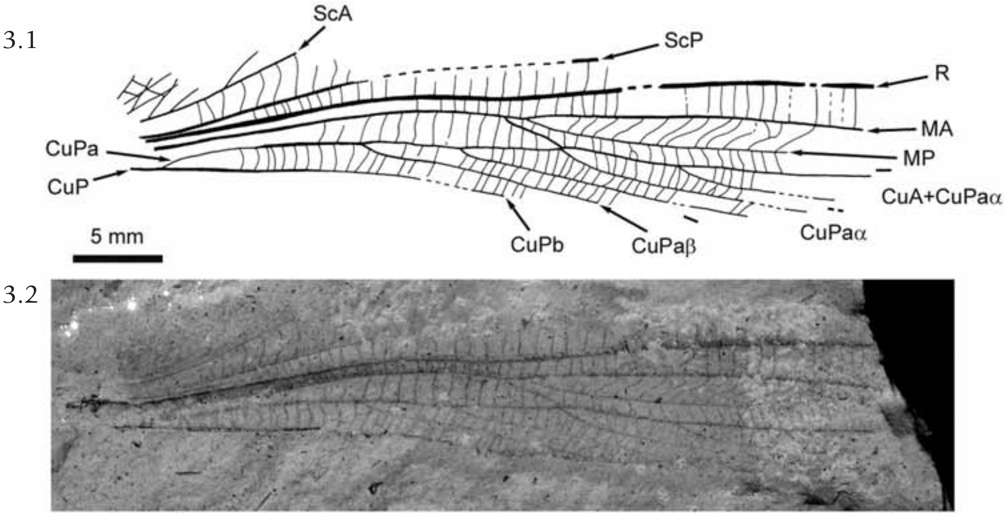


**Fig. 3.** *Tcholmanvissia longipes*, specimen PIN 1700/1531 (counterpart).

3.1: reconstruction of the left forewing (reversed).

3.2: photography (counterpart, under alcohol).

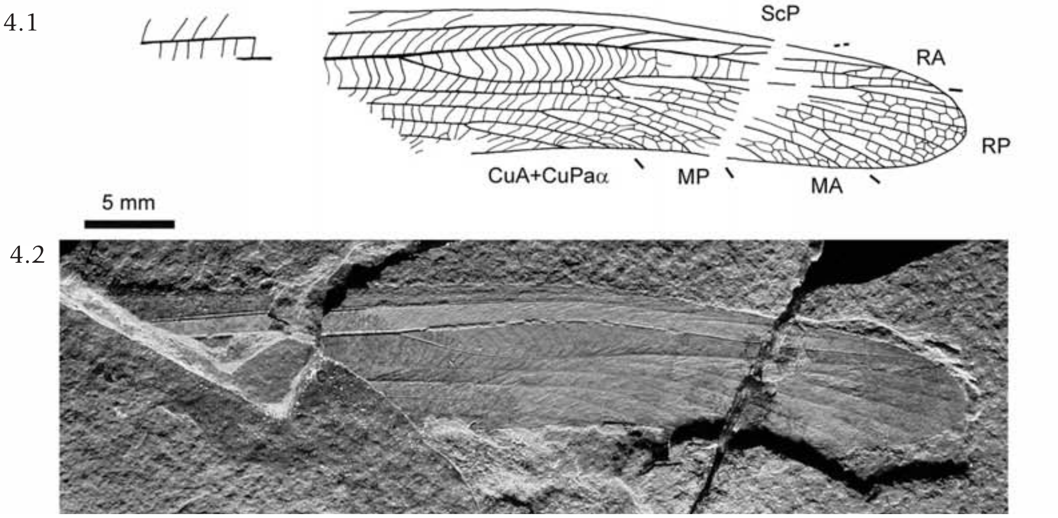


**Fig. 4.** *Tcholmanvissia longipes*, specimen PIN 1700/1454 (part and counterpart).

4.1: reconstruction of the left forewing (reversed).

4.2: photography (counter part, light-mirrored).

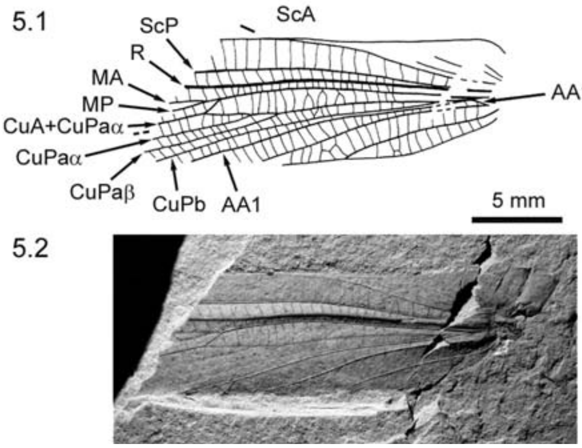


**Fig. 5.** *Tcholmanvissia longipes*, specimen PIN 1700/1483 (part and counterpart; holotype of *zalesskyi* species).
5.1: reconstruction of the left forewing.
5.2: photography (part).

Specimen PIN 1700/1483 (Fig. 5): Part and counterpart of the very basal part of a left forewing; width opposite end of ScA on anterior margin 7.0 mm; anterior wing margin very weakly posteriorly bowed in 'precostal' area; origin of posterior branch of CuPaα 1.5 mm distal of origin of CuPaα; anterior branch of CuPaα 2.5 mm long before its connection with CuA; first fork of CuA + CuPaα distal of origin of this vein; AA1 and AA2 originating from a common stem; AA1 oriented towards anterior margin at its origin, shortly fused with CuP, and running close to CuP in its proximal half.

*Occurrence.*— Tshekarda locality (Urals, Russia), Kungurian (Early Permian) (Rasnitsyn & Zherikhin 2002).

*Remark.*— The posterior branch emerging at connection of CuPaα with CuA, visible in the specimens PIN 1700/1488 and PIN 1700/1531, is interpreted as a posterior branch of CuPaα. Nevertheless, this homology is debatable because this branch could be also interpreted as a branch of CuA + CuPaα. In any case, this debate is of little interest, because the other specimens attributed to this species share the diagnostic '1 or 2 basal posterior branch(es) of CuPaα occurring just basal of its connection with CuA'. These branches have variable positions. It is also the case for the first nonambiguous fork of CuA + CuPaα. The branching pattern of CuPaα in this genus (see below) is variable, with the occurrence of a posterior branch of CuPaα basal of or opposite to the connection with CuA.

### *Tcholmanvissia noinskii* Zalessky 1929
Figs 6-9

*Tcholmanvissia noinskii* – Zalessky 1929, p. 19-21, Fig. 8 (original description).
*Tcholmanvissia noinskii* – Zalessky 1932, p. 187-188, text-Fig. 3, pl. XIII, Fig. 3 (redescription with photograph).
*Tcholmanvissia explicator* – Zalessky 1934, p.154-155, Fig. 3 (additional material assigned to a new species).
*Pinegia zalesskyi* – Gorochov 1987, p. 79, Fig. 1.e (additional material assigned to a new species).
*Pinegia martynovi* – Gorochov 1987, p.79, Fig. 1.f (additional material assigned to a new species).
*Pinegia martynovi* – Gorochov 1995, Fig. 162 (material figured).

*Material.*— Location of type specimen unknown, perhaps in the Vernadsky State Geological Museum (Moscow), with other fossil insects described by G. Zalessky; other examined material: PIN 3353/391, PIN 117/258, PIN 3353/381 and PIN 3353/396, housed in Paleontological Institute, Russian Academy of Sciences (Moscow).

*Discussion on specific synonymy list.*— After the available information on intraspecific variation yielded by specimens of *T. longipes*, the specific synonymy of *T. noinskii*, *T. explicator*, *P. zalesskyi*, and *P. martynovi* is well supported. After Zalessky M.D. (1929) and Zalessky G.M. (1934), the estimated width of the forewings of *T. noinskii* and *T. explicator* are about 15 mm. This size agrees with the material we could examine. Consequently, this species differs from *T. longipes* by its broader forewing.

The specimens from Soyana river (Iva-Gora formation; age identical to Tikhie Gory) that Gorochov attributed to *P. zalesskyi* and *P. martynovi*, plus additional material described below, share the same forewing width as *T. noinskii*. The species '*P. zalesskyi*' and '*P. martynovi*' cannot be differentiated from this last species, *contra* Gorochov (1987) who provides insufficient diagnoses, given the variability within the genus (see above).

*Diagnosis.*— Forewing width exceeding 15 mm; CuPa branching into CuPaα and CuPaβ, basal of end of ScA on anterior wing margin.

*Redescriptions.*— Specimen PIN 3353/391 (holotype of *P. zalesskyi*) (Fig. 6): Part and counterpart of an incomplete left forewing, with most of 'precostal' area, apex, base and anal area missing; preserved wing length 57.2 mm, estimated wing length about 77 mm, width 15.8 mm; ScA convex, sigmoidal; area between ScA and anterior wing margin with branched veins; ScP concave; cross-veins between ScA and ScP straight, regularly spaced, without reticulation; cross-veins (branches?) between ScP and anterior wing margin distal of end of ScA on anterior margin more and more oblique, most of them being simple, with secondary cross-veins between them; R slightly undulated in basal third of wing (anteriorly bowed basally and posteriorly bowed opposite origin of CuA from M + CuA); R and RA strongly convex; RA anteriorly pectinate 12.9 mm after origin of RP, with very probably more than 5 branches, one of them being branched in its preserved part; cross-veins between ScP and RA more and more sigmoidal from base to apex; area between RA and RP broadened, with max. width (3.2 mm) roughly opposite first branches of RA, RP and MA; cross-veins reticulated in wider part of this area, bowed towards apex in narrower part; RP branched, not distinctly concave; M + CuA anteriorly bowed before separation of M and CuA; M very short (1.2 mm) before origin of MA; MA without pronounced relief, distally ramified, with at least 3 branches; MP concave, simple in preserved part; area between MA and MP broadened, with strongly sigmoidal cross-veins in widest part; anterior branch of CuPaα long (3.5 mm) and CuA short (1.8 mm) before their connection; anterior branch of CuPaα basally concave and distally convex; CuA + CuPaα posteriorly pectinate, with 5 simple (very probably) branches; first branch of CuA + CuPaα 4.0 mm distal of origin of CuA + CuPaα; cross-veins in areas between branches of CuA + CuPaα, posterior branch of CuPaα and CuPaβ straight (in the middle of wing) to sigmoidal (near posterior margin), weakly spaced, subparallel to posterior wing margin; anterior branch of CuA + CuPaα distinctly convex; free posterior branch of CuPaα, CuPaβ, CuPb and AA1 simple, a very small part of the distinctly convex AA1 being visible.

**Fig. 6.**
*Tcholmanvissia noinskii*, specimen PIN 3353/391 (part and counterpart; holotype of *zalesskyi* species).

6.1: reconstruction of the left forewing.

6.2: photography (part).

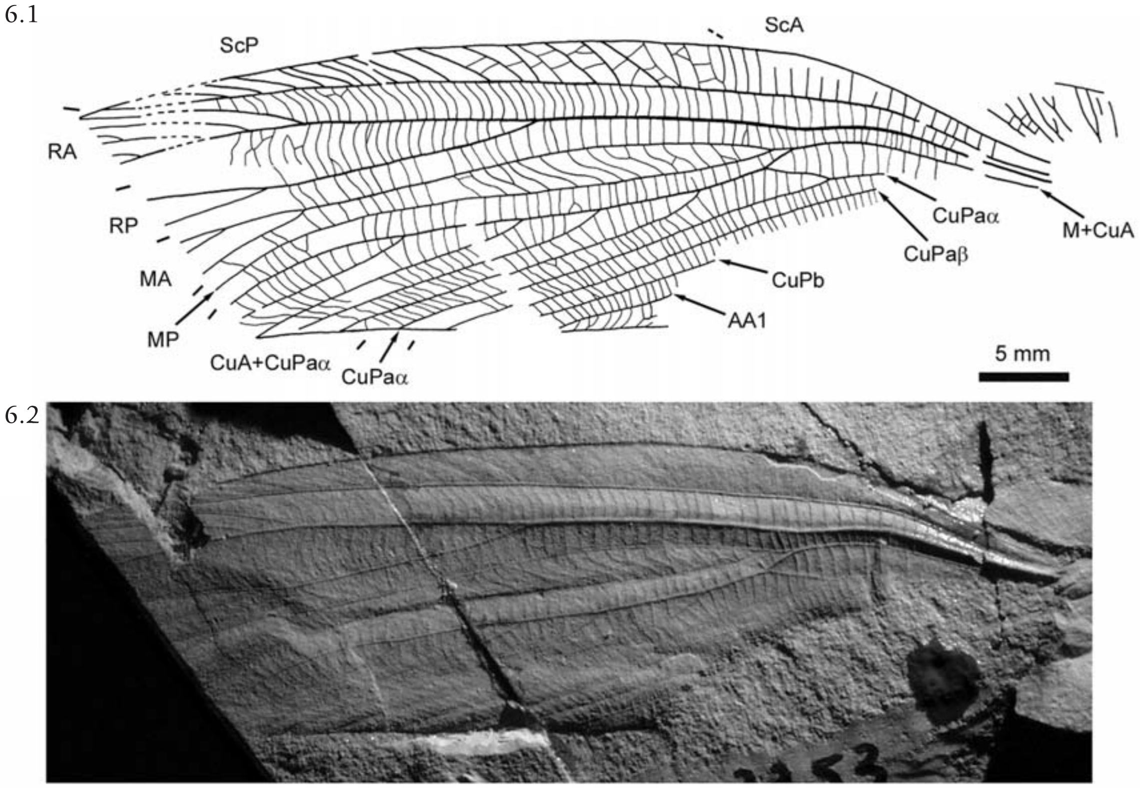


**Fig. 7.**
*Tcholmanvissia noinskii*, specimen PIN 117/258 (counterpart) and 117/259 (part) (holotype of *martynovi* species).

7.1: reconstruction of the left forewing.

7.2: photography (counterpart, light-mirrored).

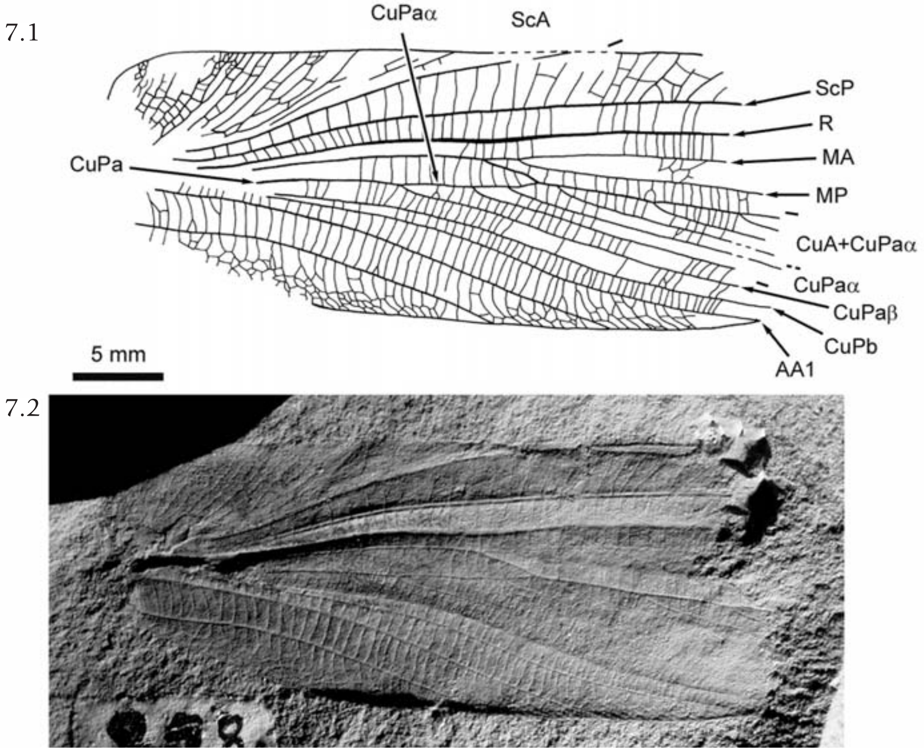
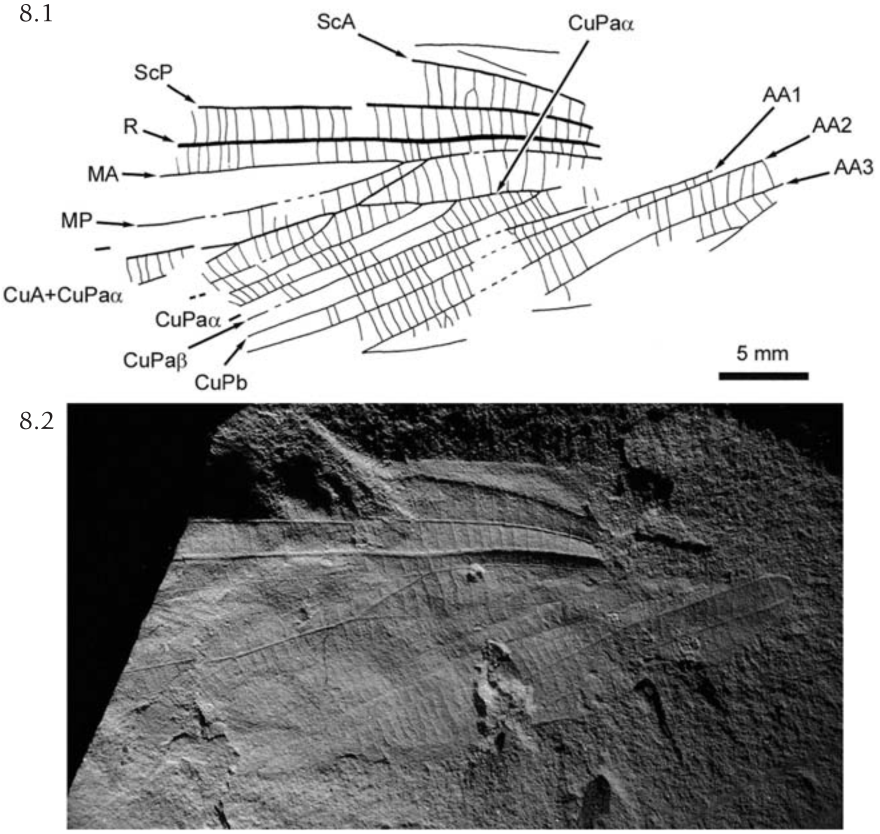


**Fig. 8.**
*Tcholmanvissia noinskii*, specimen PIN 3353/381 (counterpart).

8.1: reconstruction of the right forewing.

8.2: photography (counterpart, light-mirrored).



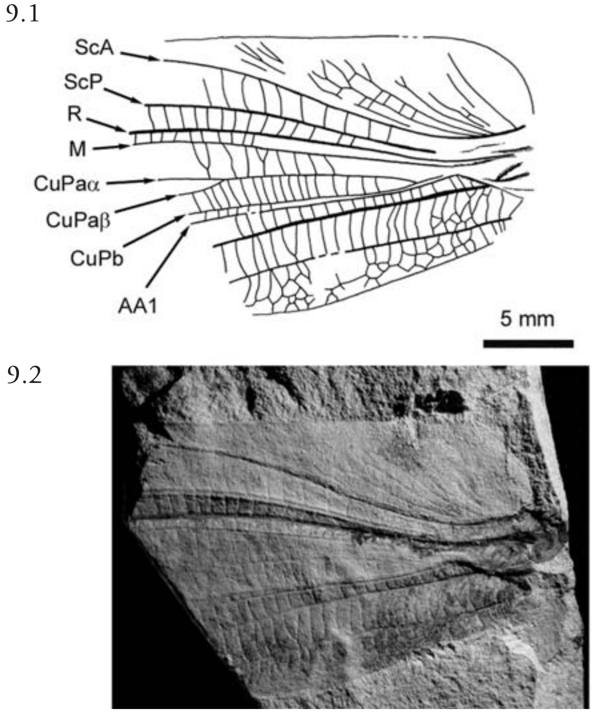


**Fig. 9.** *Tcholmanvissia noinskii*, specimen PIN 3353/396 (part and counterpart).
9.1: reconstruction of the left forewing.
9.2: photography (counterpart).

Specimen PIN 117/258 (counterpart) and 117/259 (part) (holotype of *P. martynovi* species) (Fig. 7): Incomplete left forewing (about 2 distal thirds missing); width 15.5 mm; area between anterior margin and ScA with numerous branched and reticulated veins, and with numerous cross-veins between them; CuPaα with 2 free additional posterior branches before connection with CuA: first posterior branch occurring 4.0 mm distal of origin of CuPaα, and second posterior branch 2.0 mm distal of origin of first one and 1.6 mm basal of fusion of CuPaα with CuA; first branch of CuA + CuPaα 1.2 mm distal of origin of CuA + CuPaα; AA1 very close to CuPb at wing base; area between AA1 and CuPb always narrower than area between AA1 and AA2; AA2 and AA3 more distinctly convex than AA1; areas between anal veins with reticulated cross-veins near posterior margin; all anal veins simple.

Specimen PIN 3353/381 (Fig. 8): Counterpart of a very incomplete right forewing; width 17.1 mm; CuA 4.5 mm long before its fusion with CuPaα; CuPaα 4.7 mm long before its first branch; second branch of CuPaα 2.0 mm distal of first one and 3.4 mm basal of fusion of CuPaα with CuA; first branch of CuA + CuPaα 1.5 mm after origin of CuA + CuPaα.

Specimen PIN 3353/396 (Fig. 9): Part and counterpart of the very base of a right forewing; visible part of anterior margin of 'precostal' area straight; origins of branches of ScA in very basal positions; separation of CuPa and CuPb very basal; CuPa long (10.6 mm) before origin of CuPaα and CuPaβ; base of AA1 not visible, located below a bulge (on counterpart); visible origins of AA1 and CuP distinct but very close; AA1 running close to CuP and CuPb.

*Occurrence.*— Holotypes of *T. noinskii* and *T. explicator*: Tikhije Gory (Tatarian Republic, Russia), Kazanian (Late Permian); specimens PIN 3353/391, PIN 117/258, PIN 3353/381 and PIN 3353/396: Soyana locality (Arkhangelsk Region, Russia), Kazanian (Late Permian) (Gorokhov 1987, Rasnitsyn & Zherikhin 2002).

*Remarks.*— The relative positions of the branches of CuPa and the apex of ScA on the anterior margin are not preserved in most specimens. But *T. noinskii* and *T. longipes* can be differentiated mainly by their different sizes. Of course, statistical tests cannot be made because of the limited available material. But this character seems secure enough because the difference ratio is high (*T. longipes* forewing width is about 70% of that of *T. noinskii*), without any known intermediate specimen. Moreover, the two sets of specimens differ in age, which is an additional support for specific separation.

### *Jubilaeus* Sharov 1968

*New diagnosis.*— Forewings: Distinctly broader and longer than *Tcholmanvissia* (ratio about 1.2 in respect to *T. noinskii*, species with largest wings) but narrower than *Tcholmanvissiella*; posterior wing margin straight, without inflexion opposite its distal third; cross-veins in area between MA and MP straight; MA with numerous posterior branches (10 in type specimen but variability unknown); CuPaβ branched; AA1 distally branched; irregular net of cross-veins in areas between branches of RP, MA, MP and CuA + CuPaα in distal third of wing, with more than two ranks of cells occurring in apical part.

*Composition.*— Type-species *Jubilaeus beybienkoi* Sharov 1968 (Late Kungurian, Early Permian; Chekarda, Russia).

### *Jubilaeus beybienkoi* Sharov 1968
Fig. 10

*Material.*— Holotype specimen PIN 1700/4126, housed in Paleontological Institute, Russian Academy of Sciences (Moscow).

*Diagnosis.*— That of the genus (see above).

*Occurrence.*— Tshekarda locality (Urals, Russia), Kungurian (Early Permian) (Sharov 1968, Rasnitsyn & Zherikhin 2002).

*Remark.*— Despite the accurate drawing in Sharov (1968: Fig. 11.B) and photograph in Gorochov & Rasnitsyn (2002: Fig. 434), we illustrate this taxon in order to facilitate its comparison with the other Tcholmanvissiidae and to illustrate the diagnostic branching of CuPaα: AA1 is easily recognizable from its marked convexity (Fig. 10.2). This allows us to homologize the 3 branches of CuP before its connection with CuA as CuPb, CuPaβ and an additional posterior branch of CuPaα. Nevertheless, a full redescription is not necessary.

### *Tcholmanvissiella* Gorochov 1987

*New diagnosis.*— Forewing: Distinctly broader and longer than other Tcholmanvissiinae; area between RA and RP broadened; posterior branch of CuPaα posteriorly pectinate with numerous branches; CuPaβ branched; cross-veins between branches of free part of CuPaα very close, sigmoidal and subparallel to posterior wing margin (the organization usually occurring between branches of CuA + CuPaα in other 'oedischioids'); CuA + CuPaα with few (3) branches; cross-veins in basal half of area between MA and MP moderately sigmoidal.

*Composition.*— Holotype species *Tcholmanvissiella gigantea* Gorochov 1987 (Early Kazanian, Late Permian; Iva-Gora beds, Arkhangelsk region, Russia).

### *Tcholmanvissiella gigantea* Gorochov 1987
Fig. 11

*Material.*— Holotype specimen PIN 3353/78, housed in Palaeontological Institute, Russian Academy of Sciences (Moscow).

*Diagnosis.*— That of the genus.

*Redescription.*— Holotype specimen PIN 3353/78 (Fig. 11): Part and counterpart of an almost complete and perfectly preserved right forewing with part of anal area, apex, and base of wing missing; preserved length 92.6 mm, estimated length at least 110 mm (about 125 mm if shape of apical area is similar to that of *T. longipes*), width 26.9 mm; ScA convex, long, sigmoidal, approximately anterior wing margin in length; origin of branches of ScA not well discernable, very basal for most of them; branches of ScA numerously branched, with a very dense net of cross-veins between them; cross-veins between ScA and ScP with very few reticulations basal of end of ScA on anterior margin; cross-veins between ScP and anterior wing margin with intercalary cross-veins between them; ScP concave, long, reaching anterior wing margin about 88.9 mm distal of wing base; R very strongly marked, distinct from M in preserved part; origin of RP 47.3 mm distal of wing base; RA strongly marked, convex, branched about 30.2 mm distal of its origin, anteriorly pectinate, with at least 6 branches, all simple in preserved part; area between them narrow, with short straight and regularly spaced cross-veins; cross-veins between ScP and RA gradually straight (in basal part) to sigmoidal (in distal part); RP with no marked relief (neutral), distally branched (32.0 mm distal of its origin), just distal of first branching of RA; RP posteriorly pectinate in preserved part, with at least 3 branches; area between RA and RP broadened, max. width 5.7 mm opposite first branch of RA; in its wider part, cross-veins between RA and RP irregularly reticulated (no distinct central row of cells); CuA emerging from M + CuA about 33.0 mm distal of wing base; M very short (1.1 mm) before origin of MA; MA with numerous branches (first fork 19.0 mm after its origin), roughly dichotomous; MP distinctly concave, branched very distally and dichotomously in preserved part; CuP and branches of CuP distinctly concave but only in basal part; separation of CuPaα and CuPaβ 9.8 mm distal of origin of CuPa; CuPaα branched 6.5 mm after its origin; free CuA slightly sigmoidal, 3.1 mm long before its connection with CuPaα; CuPaα very long (7.8 mm) before its connection with CuA; CuA + CuPaα with only 3 branches; posterior branch of CuPaα posteriorly pectinate, with 4 simple branches; CuPaβ with 2 branches, the most anterior one being fused at length with the most posterior branch of CuPaα; CuPb, AA1 and AA2 simple in preserved parts; AA1 convex, very close to CuP at its origin; AA2 convex, with a relief more marked than AA1; cross-veins in areas between branches of RP and M reticulated distal of first branching of RA (roughly distal of max. width of area between RA and RP, distal of first branch of RP); cross-veins in basal part of area between MA and MP slightly sigmoidal; close to posterior wing margin, cross-

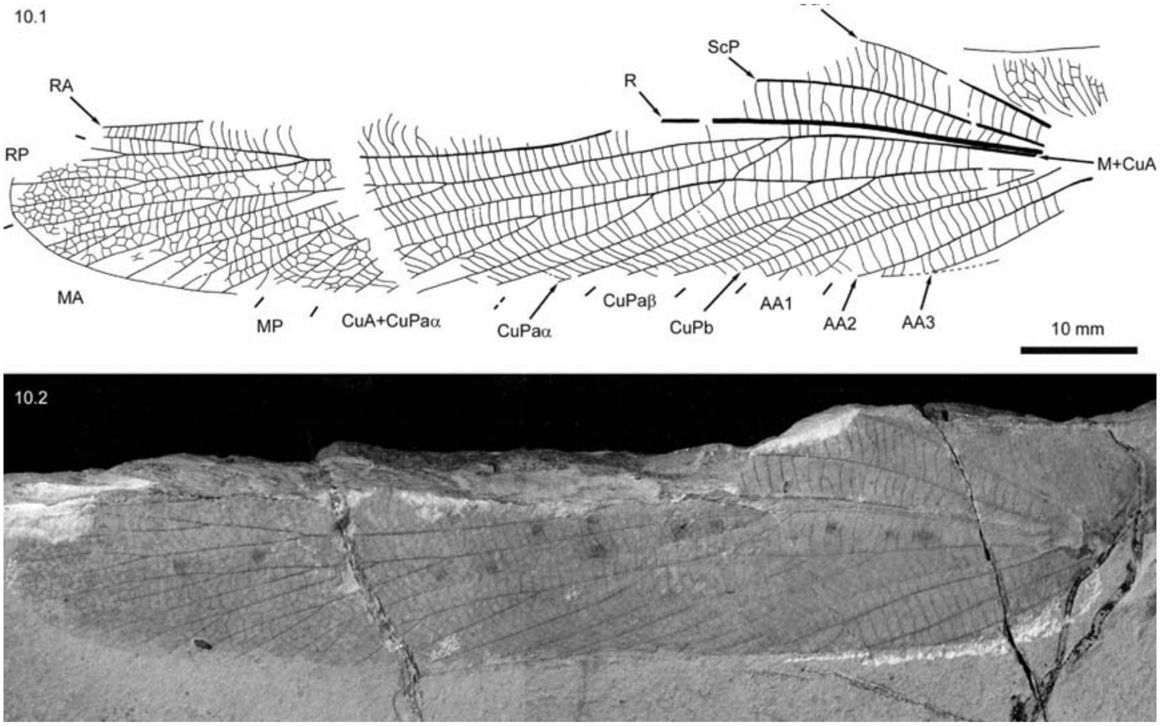


**Fig. 10.** *Jubilaeus beybienkoi*, specimen PIN 1700/4126 (holotype; part and counterpart).
10.1 : reconstruction [coloration (maculae) omitted].
10.2 : photography (part).

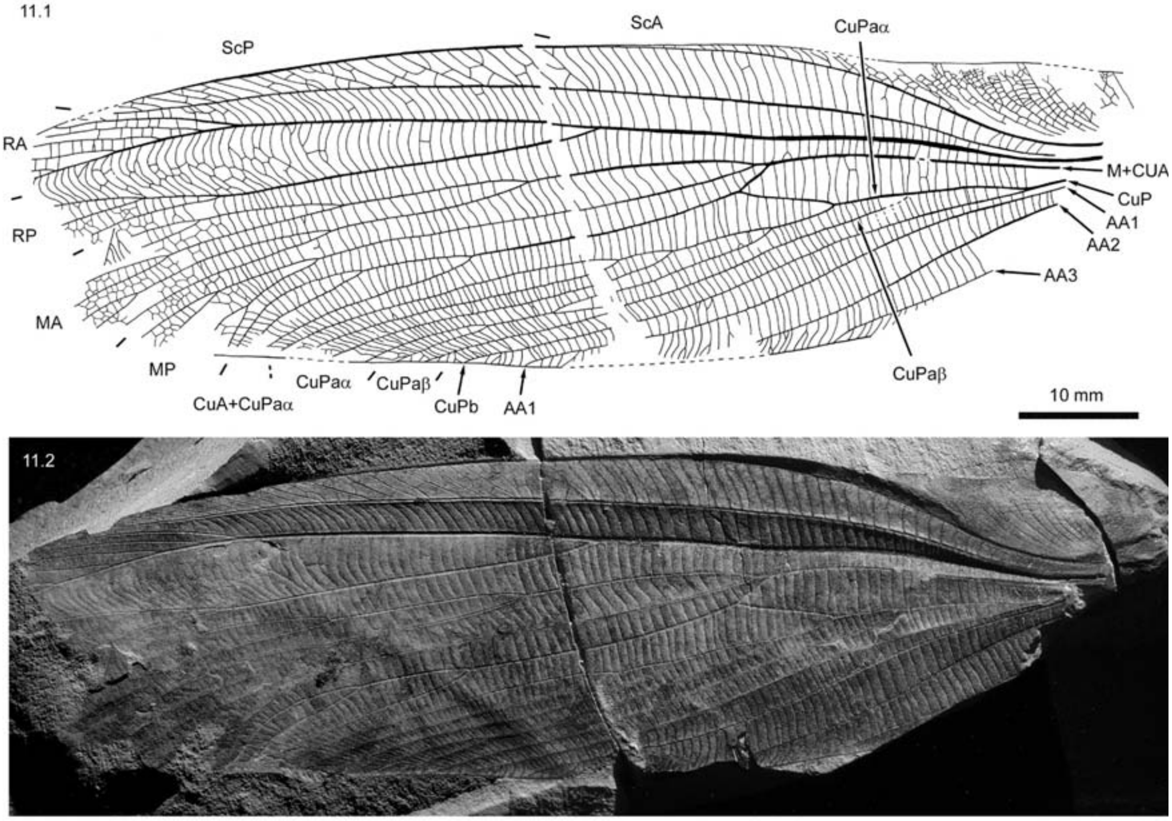


**Fig. 11.** *Tcholmanvissiella gigantea*, specimen PIN 3353/78 (holotype; part and counterpart).
11.1 : reconstruction of the right forewing.
11.2 : photography (counterpart).

veins between branches of CuA + CuPaα and posterior branches of CuPaα very approximate, sigmoidal, and subparallel to wing margin; cross-veins in others areas of wing straight, rarely reticulated, and regularly spaced.

*Occurrence.*— Soyana locality (Arkhangelsk Region, Russia), Kazanian (Late Permian) (Gorokhov 1987, Rasnitsyn & Zherikhin 2002).

*Remark.*— Despite the original drawing of Gorochov (1987) and photograph of the fossil published in Gorochov & Rasnitsyn (2002: Fig. 433), several errors in descriptions render necessary the present new figure and redescription.

*T. gigantea* is among the largest known Orthoptera *sensu stricto* (see http://tolweb.org/tree/eukaryotes/animals/arthropoda/hexapoda/orthoptera/orthoptera.html for size ranges in extant Orthoptera).

### Phylogenetic relationships of the Tcholmanvissiidae

The assignment of Tcholmanvissiidae to Orthoptera is well-supported: 1) the holotype of *T. longipes* has jumping legs with broadened femora (Martynov 1940: Fig. 36); 2) all representatives of this family share the 'oedischioid' arrangement of cross-veins in areas between branches of CuA + CuPaα, where cross-veins are subparallel to the posterior wing margin and sigmoidal. Béthoux & Nel (2002) questioned the monophyly of the Tcholmanvissiinae *sensu* Gorochov (1995a), but their available information was less complete. The new data support the monophyly of the Tcholmanvissiidae as interpreted herein (see diagnosis and below).

Sharov (1968: Fig. 10) expected close relationships between Tcholmanvissiinae *sensu* Gorochov (= Tcholmanvissiidae *sensu* Sharov) and Caelifera. Despite the fact that representatives of the Tcholmanvissiinae were not included in their analysis, Béthoux & Nel (2002) demonstrated a close relationship between Caelifera and 'elcanids'. The Tcholmanvissiinae do not share the apomorphies of the Panelcanida (Béthoux & Nel 2002) and no panelcanid has apomorphies of the Tcholmanvissiidae. Until a revised cladistic analysis is performed, these taxa cannot be considered related.

Sharov also hypothesized that the Tcholmanvissiinae gave rise to the Titanoptera and the Phasmatodea. Nevertheless, Gorochov (1996, 2001) and Béthoux & Nel (2002) discussed the relationships between Phasmatodea, Titanoptera, and Orthoptera and concluded that Phasmatodea and Titanoptera were not directly related to the Orthoptera *sensu stricto*. The Tcholmanvissiinae, Phasmatodea and Titanoptera share no known apomorphic character.

Within 'oedischioids', we consider the Tcholmanvissiinae as closely related to Tettoedischiinae, as hypothesized by Gorochov (1995b). Both subfamilies share the additional branch(es) of CuPaα before its connection with CuA (for its occurrence in Tettoedischiinae, see Figs 12-13). Note that Gorochov (1995b: 86) interpreted these additional branch(es) as a branch of 'MP + CuA1' proximally fused with 'CuA1' before the fusion of 'MP' with 'CuA1'. This seems hardly possible (a branch of a vein occurring before the occurrence of the vein itself?). He also judged that the structure of 'MP + CuA1' [= CuA + CuPaα] is apomorphic of both subfamilies, but the ramifications of this vein (between *Macroedischia* and *Tcholmanvissiella*, for example).

The character 'CuPaα branched at least one time before its connection with CuA' is absent in all other Orthoptera and Panorthoptera. Until a revised cladistic analysis is performed, the apomorphic value of this character, limited to this group, has to be considered as valid. Also, because no other taxa share this character, the Tcholmanvissiidae must be considered an extinct taxon, with a known restricted period of occurrence from Late Kungurian (Early Permian) to Early Kazanian (Late Permian).

Interestingly, the best-recorded representative of the Tettoedischiinae, *M. elongata* (Figs 12-13; see Sharov 1968, Fig. 8.E for holotype) has some variability in the connection between RP and MA1. This connection is completely lost in the sister subfamily Tcholmanvissiinae. This kind of information is important for elucidating relationships within the 'oedischioids' because, in this 'group', but also in Ensifera and Caelifera, the connection of RP with MA1 is an homoplasic structure (convergently lost several times within the Orthoptera), but also a phylogenetically meaningful one when reversions can be demonstrated by a sufficient set of other apomorphies.

## Conclusion

In order to improve information about the problematic 'oedischioids' group, we undertook a systematic review of the Tcholmanvissiidae. A set of specimens attributed to *Tcholmanvissia longipes* permitted evaluation of intraspecific variability, supporting several new generic and specific synonymies. Careful examination of the type specimen of *Tcholmanvissiella gigantea* yielded new diagnostic characters. Finally, the subfamily Tcholmanvissiinae is composed of 3 genera, 2 of them being monotypic and one including 2 species.

New crucial information on relative width and relief of veins and cross-veins is given. These data permitted us to homologize the cubital vein pattern of the Tcholmanvissiinae and to establish relationships with Tettoedischiinae on the basis of a reliable apomorphy. The variability in location and number of the additional branch(es) of CuPaα is high, but at least one free branch is always present.

This study is a part of a wider review of the Palaeozoic 'oedischioids', Ensifera and Caelifera, dedicated to the resolution of the relationships of the most 'primitive' Orthoptera. It also aims to find the affinity between representatives of Panorthoptera, in order to determine outgroup(s) as closely related to Orthoptera as possible. Among others, these studies should allow a sharpening of the estimation of the divergence date between Ensifera and Caelifera.

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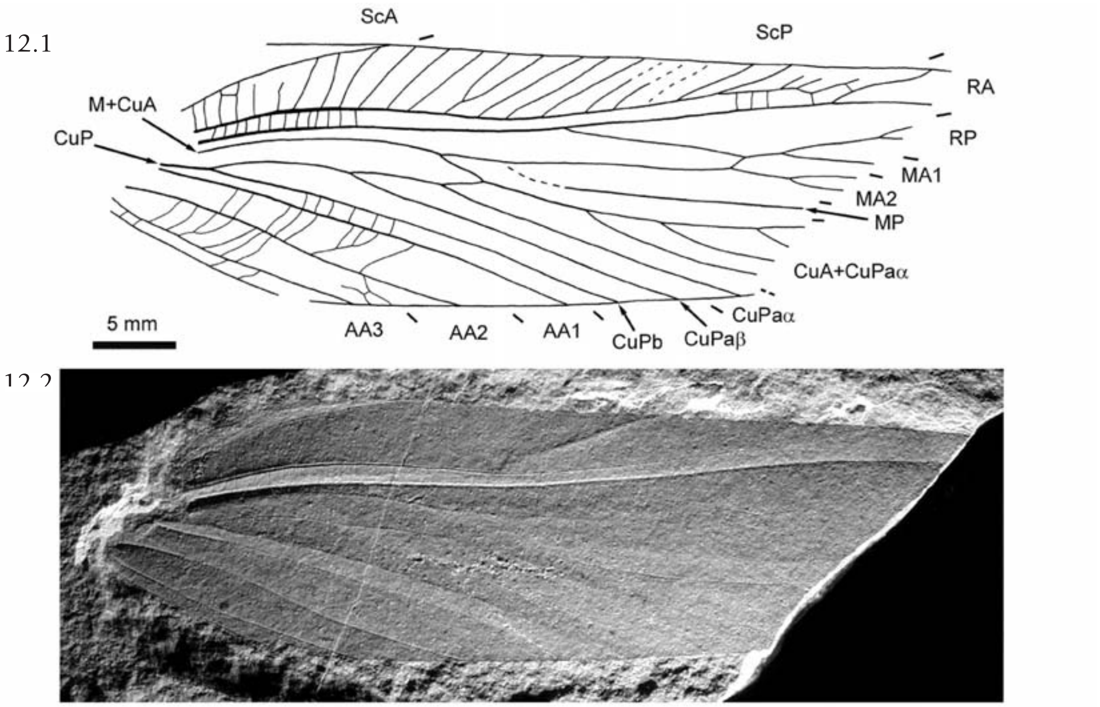

**Fig. 12.** *Macroedischia elongata*, specimen PIN 1700/4130 (paratype; part)

12.1: reconstruction of the right forewing.

12.2: photography.

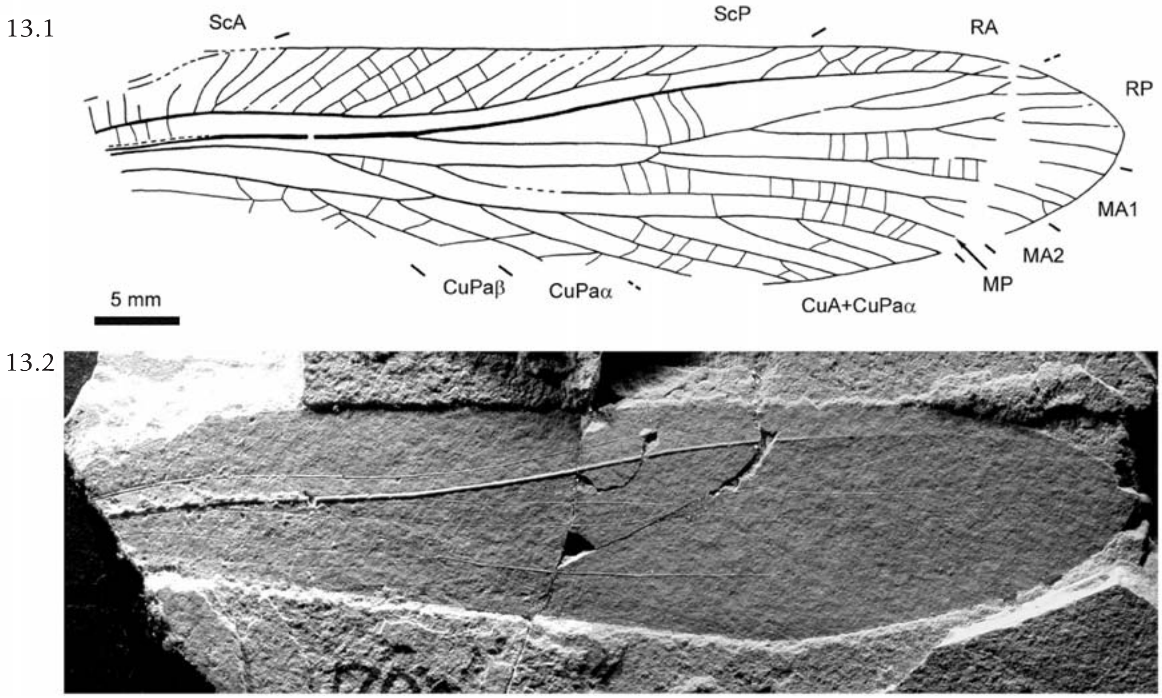

**Fig. 13.** *Macroedischia elongata*, specimen PIN 1700/4129 (paratype; part and counterpart)

13.1: reconstruction of the right forewing.

13.2: photography.

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