

Cladotypic Taxonomy Applied: Titanoptera are Orthoptera

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> Abstract

The Linnaean taxon Titanoptera is a distinctive Triassic insect order the origin of which is uncertain. Forewing venation patterns of the Permian Linnaean subfamily Tcholmanvissiinae (Orthoptera) and of the Titanoptera are re-investigated. The comparative analysis supports the view that the morphology of the latter group is derived from that of the former. As a consequence, the order Titanoptera is to be included within the subfamily Tcholmanvissiinae. A cladotypic taxonomy is developed in order to avoid the confusion inherent to taxonomic rearrangements associated with rank-based taxonomy. The following hierarchy is proposed: (*Archaeorthoptera* nom. Béthoux & Nel, 2002a, *dis.-typ.n.* (*Pantcholmanvissiida* nom. n., *dis.* Béthoux & Nel, 2002b, *typ.n.* (*Tcholmanvissiidae* nom. Zalesky, 1934, *dis.* Sharov, 1968, *typ.n.* (*Tcholmantitanoptera* nom. *dis.-typ.n.* (*Tcholmanvissiella* nom. Gorochoy, 1987, *dis.-typ.n.* (*Titanopterida* nom. *dis.-typ.n.* (*Gigatitanidae* nom. Sharov, 1968, *dis.-typ.n.*)))))). This first application of cladotypic taxonomy unveiled several practical aspects of this system. A system governing the adaptation of pre-occupied taxon names is developed based on various cases of character state formulations; the issue of the occurrence of Linnaean suffixes and of the preservation of Linnaean binomials within a cladotypic taxonomy are discussed; the capacity to handle the ancestor ‘species’ vs. apomorphy-less sister-species issue by the various nomenclatural systems is discussed.

> Key words

Pterygota, *Archaeorthoptera*, Orthoptera, Titanoptera, *Titanopterida*, cladotypic taxonomy, adaptation, priority, ancestor species.

1. Introduction

Attempts to exhaustively inform the taxonomic position of fossil stem groups would necessitate a surfeit of ranks if strictly following the traditional Linnaean rank-based nomenclatural system. Phylogenetic (CANTINO & DE QUEIROZ 2006), topology-based (SERENO 2005), and cladotypic (BÉTHOUX 2007d, e) taxonomic systems, which are all rank-less, have the advantage of avoiding this pitfall, and avoiding the need for modification of taxa names if a hierarchical re-arrangement is necessary. Therefore their use might result into more stable taxonomies. Among the alternative systems, the cladotypic approach is likely to be the most efficient, because it relies on assumptions that are more easily falsifiable than are those involved in other rank-less approaches. Moreover it is fully operative as rules are provided for the species case, unlike other alternative systems. Herein, I apply this new system to a case involving fossil taxa nested within a group having modern representatives.

I will focus on the resolution of relationships of the Linnaean order Titanoptera Sharov, 1968 (thereafter

informally referred to as titanoptera) with respect to the Linnaean order Orthoptera Olivier, 1789 (thereafter informally referred to as orthoptera). Several hypotheses on the origin of the very distinctive titanoptera were proposed. The Upper Carboniferous Linnaean family Geraridae Scudder, 1885, which is currently viewed as a close relative of orthoptera (SHAROV 1968, 1971; Gorochoy 2001; BÉTHOUX & NEL 2003; in prep.), was proposed as sister-group of titanoptera by GOROCHOV (2001), followed by BÉTHOUX (2005a: 405). On the other hand SHAROV (1968, 1971) considered that titanoptera diverged from the Linnaean family Tcholmanvissiidae (orthoptera represented during the Permian), which he viewed as a paraphyletic group. This author considered geraridaeans to be the only representatives of the Linnaean order Protorthoptera, itself understood as paraphyletic and ‘ancestral’ to the orthoptera.

My investigations of some taxa considered by SHAROV (1968) as geraridaeans (BÉTHOUX & NEL 2003; in prep.) and of representatives of the family Tchol-

manvissiidae (BÉTHOUX & NEL 2002b and herein) lead me to propose a new interpretation of the titanopterid forewing venation, presented herein. This interpretation implies that the order Titanoptera is not directly related to the family Geraridae, as I argued previously, but to the Permian family Tcholmanvissiidae. This situation implies taxonomic re-arrangement.

2. Material and Methods

Specimens referred to as PIN are housed at the Palaeontological Institute of the Russian Academy of Science (Moscow, Russia). The specimen referred to as AM is housed at the Australian Museum (Sydney, Australia). Specimens referred to as NHM are housed at the Natural History Museum (London, UK). The specimen referred to as FG is housed at the Department of Palaeontology, Freiberg University of Mining and Technology (Freiberg, Germany).

I use the wing venation nomenclature elaborated by BÉTHOUX & NEL (2002a) for *Archaeorthoptera* (see taxon definition in the systematic section), itself based on that of orthopterans (BÉTHOUX & NEL 2001). Corresponding abbreviations are repeated herein for convenience: ScA, anterior Subcosta; ScP, posterior Subcosta; R, Radius; RA, anterior Radius; RP, posterior Radius; M, Media; MA, anterior Media; MP, posterior Media; Cu, Cubitus; CuA, anterior Cubitus; CuP, posterior Cubitus; CuPa, anterior branch of CuP; CuPa α , anterior branch of CuPa; CuPa β , posterior branch of CuPa; CuPb, posterior branch of CuP; AA1: first anal. The reader who is not familiar with orthopteran and other insect wing venation nomenclature could refer to the discussion in BÉTHOUX (2005b; and references therein) and to BÉTHOUX & NEL (2002a: fig. 1b). Critics expressed by Gorochov (2005) regarding this homologization hypothesis are addressed in BÉTHOUX (2007a). Subsequent comments by RASNITSYN (2007) are addressed in BÉTHOUX (in press).

It will be demonstrated elsewhere that CuA is simple in forewings of orthopterans and of some stem-orthopterans. In other words, all branches of CuA + CuPa α as understood by BÉTHOUX & NEL (2002a) belong to CuPa α , except for the most apical branch, which is composed of CuA and the ultimate branch of CuPa α . This homologization is applied herein. In order to make the comparative discussion easier to follow, I use the following vein abbreviations: CuPa α $^{\circ}$ (indicated by $^{\circ}$ in Fig. 1) refers to the anterior branch of CuPa α resulting from the second branching of this vein; CuPa α * (indicated by * in Fig. 1) refers to the posterior branch of CuPa α resulting from the second branching of this vein; CuPa α * (indicated by * in Fig. 1) refers to the posterior branch of CuPa α resulting from the first branching of this vein.

The restoration provided in Fig. 1C is primarily based on a high-resolution photograph of the specimen AM F.36274. It was complemented by drawings drawn with a stereomicroscope and camera lucida of the specimens NHM In. 37340, NHM In. 37341, and NHM In. 37342 (Fig. 2A–C, respectively), belonging to the same species. The shape of the area between the anterior wing margin and ScA is unknown in this species and is inferred from related taxa. The restoration provided in Fig. 1D is based on the restoration of SHAROV (1968: fig. 52B), but is skewed by 16° in order to present a more plausible shape of the forewing (corresponding fossils were deformed during or after fossilisation; SHAROV 1968; RASNITSYN 1982). In other cases venation patterns and vein widths were drawn with a stereomicroscope and camera lucida direct from the fossil surface, both dry and under ethanol (except for material from Madygen, Russia, that could be damaged by ethanol immersion). Drawings were readjusted on photographs using image-editing software.

In the systematic section, I use the cladotypic taxonomic system elaborated by BÉTHOUX (2007d, e) for taxa other than species, and follow the suggestions of DAYRAT et al. (2004; and references therein) for species names. The use of the suffix ‘Pan’ is not related to the rules of the PhyloCode governing the use of ‘panclades’ (or panclade names; CANTINO & DE QUEIROZ 2006; see also JOYCE et al. 2004). Throughout this contribution, taxa understood as taken from the Linnaean system are indicated by the mention of their rank.

3. Results

3.1. Comparative morphological analysis

SHAROV (1968) proposed a homologization of the wing venation of titanopterans that has been followed by all subsequent authors (CARPENTER 1992; GOROCHOV 1995, 2003). BÉTHOUX & NEL (2002a) proposed to ‘translate’ Sharov’s nomenclature into an alternative one, intended to allow the wing venation of orthopterans to be compared to that of other winged insects. However, the authors agreed with Sharov’s interpretation of titanopteran wing venation pattern with respect to that known in orthopterans. Basically, between the veins CuA + CuPa α (Sharov’s MP + CuA $_1$) and AA1 (1A), two concave veins occur; as in orthopterans these are likely to be CuPa β (CuA $_2$) and CuPb (CuP). This is the most parsimonious interpretation if one refers only to the data accessible to Sharov.

This homologization is now challenged by my interpretation of the forewing venation of *beybienkoi* Sharov, 1968 (orthopteran assigned to the genus *Jubilaus* Sharov, 1968; Fig. 1A), *gigantea* Gorochov,

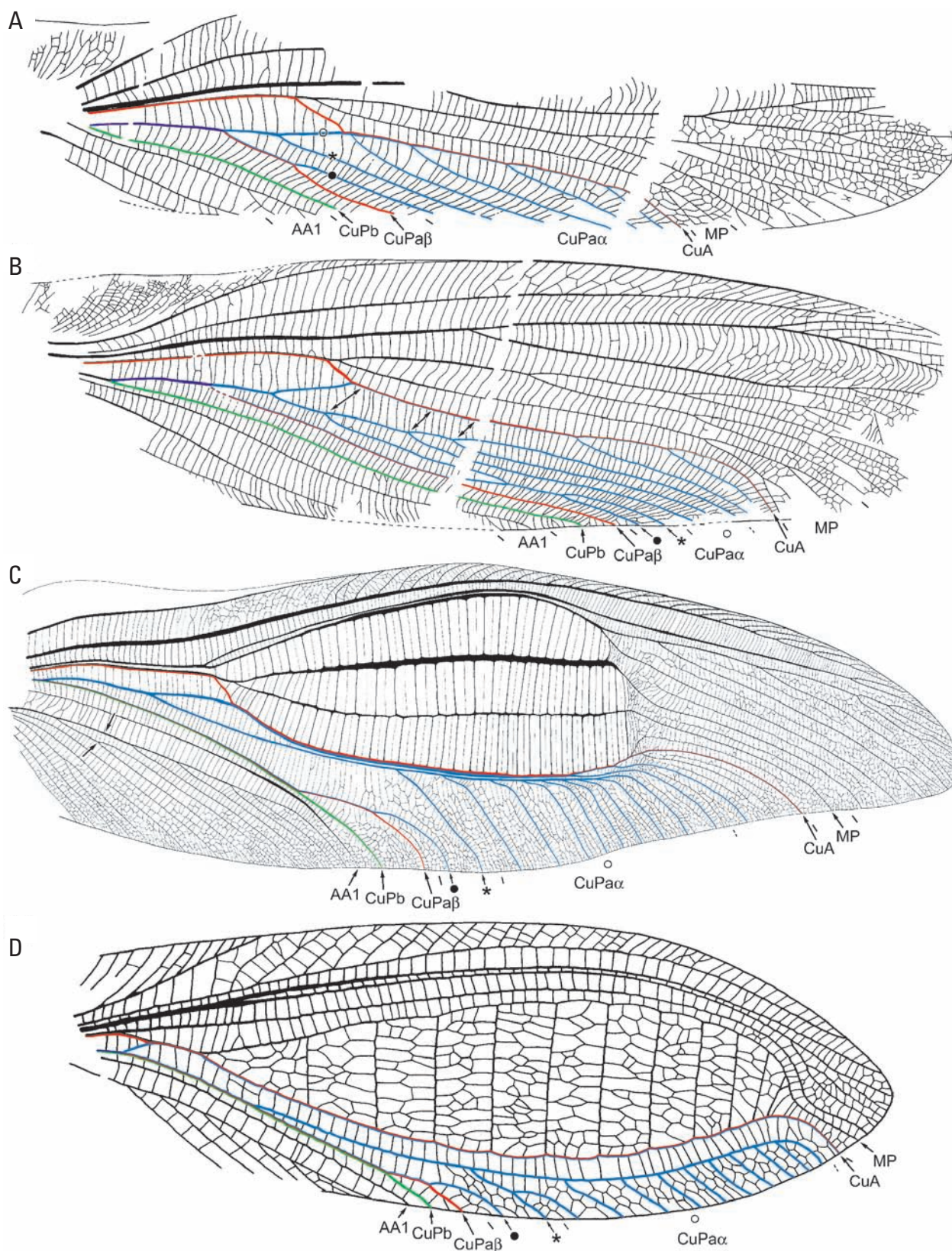


Fig. 1. Forewing venation homologies in *Pantcholmanvisiida* *nom.n., dis.* Béthoux & Nel, 2002b, *typ.n.*; orange, CuA vein; purple, CuPa vein; blue, CuPa α vein; red, CuPa β vein; green, CuPb vein (see text for abbreviations); **A:** *beybienkoi* Sharov, 1968 (from BÉTHOUX & NEL 2002b); **B:** *gigantea* Gorochoy, 1987 (from BÉTHOUX & NEL 2002b); **C:** *giganteus* Tillyard, 1916 (restoration; see text); **D:** *extensus* Sharov, 1968 (modified from SHAROV 1968: fig. 52B).

1987 (orthopteran assigned to the genus *Tcholmanvisiella* Gorochoy, 1987; Fig. 1B), and of titanoperans

(Fig. 1C–D). Together with some other species, the two former species were assigned to the family Tchol-

manvissiidae by GOROCHOV (1987) and BÉTHOUX & NEL (2002b) (thereafter informally referred to as 'tcholmanvissiidaeans'). As do other tcholmanvissiidaeans, *beybienkoi* and *gigantea* exhibit one or several posterior branches of CuPa α occurring basal to the connection with CuA (BÉTHOUX & NEL 2002b). This is a strict apomorphic character state within Neoptera. The main difference between *gigantea* and other tcholmanvissiidaeans relies on the apparent occurrence of branches of CuPa α * (it is simple in other tcholmanvissiidaeans). Additionally, *gigantea* exhibits another important difference in that CuPa α ° is apparently simple for a long distance and emits few distal branches. However, an important point was overlooked: apparent branches of CuPa α * occur opposite the section of CuPa α ° that is apparently simple; and CuPa α ° is apparently branched distally to the last apparent fork of CuPa α *. In other words, apparent branches of CuPa α ° and CuPa α * do not co-occur at the same 'level'. Therefore I argue that proximal branches of CuPa α °, as they occur in *beybienkoi*, are homologous to branches occurring on CuPa α * in *gigantea* (see double-headed arrows on Fig. 1B). In other words, several branches of CuPa α ° were 'translocated' onto CuPa α * in *gigantea* (implying that CuPa α * is actually simple). Translocation can be defined as the fusion of a vein (sector / branch) with another from the origin of the latter, so that there is no visible basal free part of the translocated vein. Such translocations frequently occur as irregularities of the wing venation pattern, as it can be seen in the anal area of the forewing of the specimen AM F.36274 (on which is based the restoration of the corresponding part on Fig. 1C; see arrows on this figure), and in the branching pattern of CuPa α ° in the restoration given on Fig. 1D (the first posterior branch of CuPa α ° is translocated onto CuPa α *). I observed a similar translocation affecting CuA branches in forewings of several mantodean taxa (occurring as an intra-individual polymorphism; pers. obs). As observed in *gigantea*, the translocation of several branches is the mere result of multiple single vein translocations.

I propose to characterize the organization of CuA and CuPa α exhibited by *gigantea* as 'in forewing, at least one proximal branch of CuPa α ° is translocated onto CuPa α *' (provided that CuPa α is branched). As defined, it applies to titanopterans (Fig. 1C–D; SHAROV 1968; GOROCHOV 2003; GRIMALDI & ENGEL 2005). In the specimen AM F.36274, the point of divergence of the first posterior branch of CuPa α ° emitted from CuA + CuPa α ° (thereafter referred to as CuA + CuPa α ° *in part*) is located basal to the last fork of branches CuPa α ° translocated onto CuPa α * (thereafter referred to as CuPa α ° *trans.*), unlike in the conspecific specimens NHM In. 37340 (Fig. 2A) and NHM In. 37342 (Fig. 2C), where the point of divergence of the first posterior branch of CuPa α ° *in part* is located op-

posite to the last fork of CuPa α ° *trans.* Therefore, I assume that the condition exhibited by the specimen AM F.36274 is due to an infra-specific variation. In some taxa from Madygen (Russia) described by SHAROV (1968, 1971) and GOROCHOV (2003), the point of divergence of the first posterior branch of CuPa α ° *in part* is located opposite to the last fork of CuPa α ° *trans.* seemingly 'overlap', but this could be due to a skewing post-depositional deformation (deformation during compaction and/or tectonic deformation affected specimens from Madygen; SHAROV 1968; RASNITSYN 1982). In conclusion I argue that the apparent branches of CuPa α * as exhibited by titanopterans are homologous to the proximal branches of CuPa α ° as exhibited by *beybienkoi*.

Once the possibility that vein branches could translocate onto a surrounding vein is admitted, it can be assumed that the vein designated as CuPa β in BÉTHOUX & NEL (2002b: figs. 10, 11) and considered as branched in *beybienkoi* and *gigantea* is merely composed of a simple CuPa β fused with the first posterior branch of CuPa α (CuPa α *). In *noinskii* Zalesky, 1929 and *longipes* Martynov, 1940 (tcholmanvissiidaeans both assigned to the genus *Tcholmanvissia* Zalesky, 1929), several individuals exhibit multiple posterior branches of CuPa α emitted before the fusion of this vein with CuA (BÉTHOUX & NEL 2002b: figs. 2, 7, 8). Additionally, in most titanopterans, the point of divergence of CuPa β and CuPa α * is located basal to the section of CuPa α ° *trans.* + CuPa α * that is simple (SHAROV 1968; Figs. 1C–D, 2B). This is reminiscent of and supported by the case discussed above. It must be noticed that no CuPa β was identified on the specimen NHM In. 37340 (Fig. 2A).

We are left with the fact that three main stems occur between CuA + CuPa α ° *in part* and AA1 in *gigantea* (CuPa α ° *trans.* + CuPa α *, CuPa α * + CuPa β , and CuPb), while only two occur in titanopterans (SHAROV 1968; Figs. 1C, 2A–B; only one occurs in *extensus* Sharov, 1968, see below). The solution can be readily found: CuPa α * + CuPa β and CuPb are fused at their origin and diverge after some distance in titanopterans, a fact evidenced by the very oblique origin of CuPa α * + CuPa β (i.e. CuPa α * + CuPa β is translocated onto CuPb). Moreover, alike in *gigantea* and *beybienkoi*, CuPa α * + CuPa β can readily be identified in titanopterans after its fork (which is the point of divergence of CuPa α * and CuPa β ; see SHAROV 1968; Figs. 1C–D, 2B). Hence the vein CuPb is simple under this new homologization.

At this step describing the forewing venation pattern of *extensus* Sharov, 1968 (see Appendix 3 for validity of related species; Fig. 1D) is a pinnacle. Besides the fact that M + CuA separates into MA and MP + CuA, that the latter fuses for some distance with CuPa α ° *in part* [resulting into a (MP + CuA) + CuPa α ° *in part*

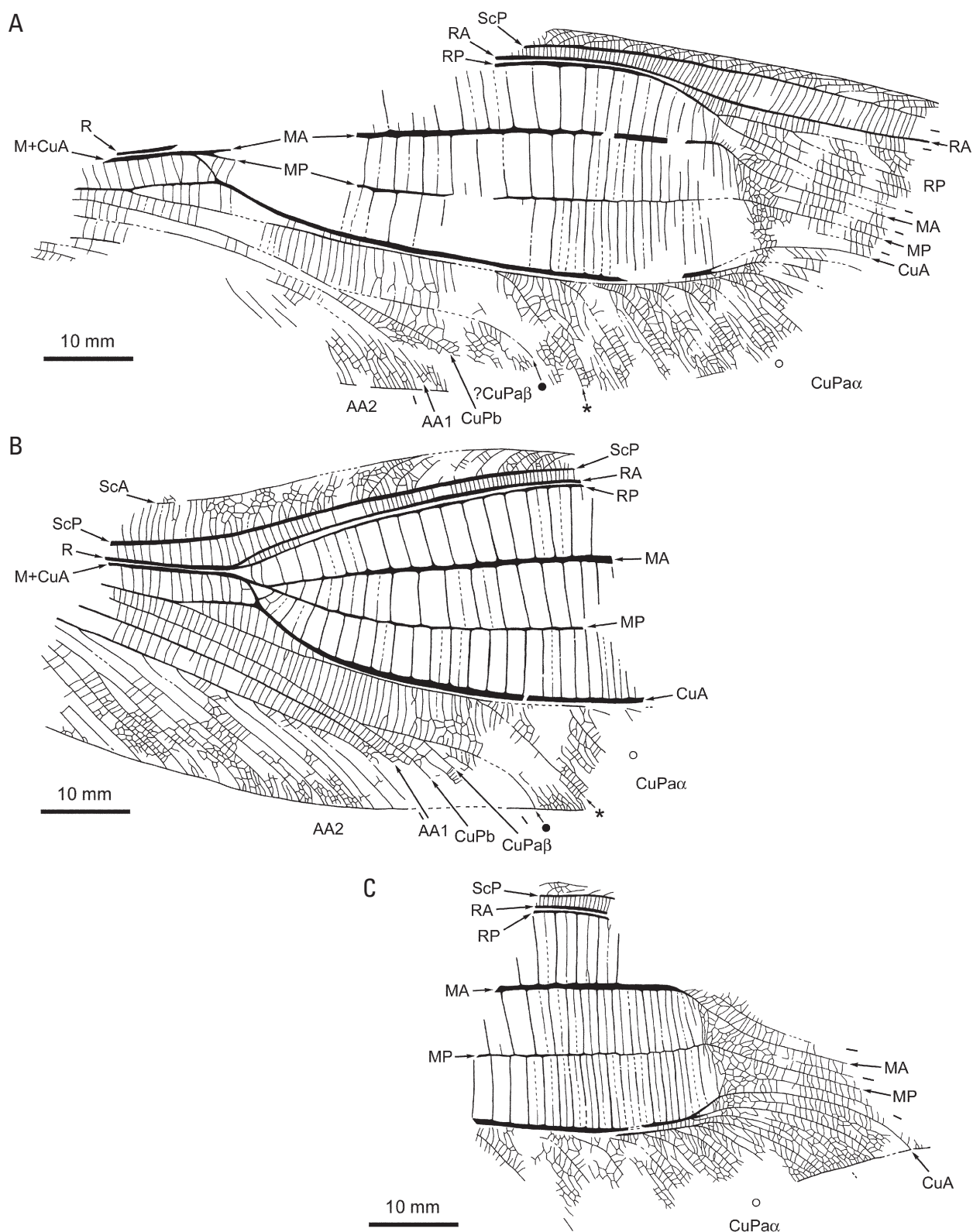


Fig. 2. Forewings of *giganteus* Tillyard, 1916, drawings of venation (see text for abbreviations). **A:** Specimen NHM In. 37340 (based on a positive imprint of a left forewing, reversed; paracladotype of *Tcholmanvissiidae* nom. Zalessky, 1934, *dis.* Sharov, 1968, *typ.n.* and *Tcholmanvissiella* nom. Gorochov, 1987, *dis.-typ.n.*). **B:** Specimen NHM In. 37341, (based on a positive imprint of a left forewing, reversed; paracladotype of *Tcholmanvissiella* nom. Gorochov, 1987, *dis.-typ.n.*). **C:** Specimen NHM In. 37342 (based on a negative imprint of a left forewing).

composite stem], and that all branches of $CuPa\alpha^\circ$ but one are translocated onto $CuPa\alpha^*$, $CuPa\alpha^\circ$ *trans.* +

$CuPa\alpha^*$ is fused with the composite stem ($CuPa\alpha^* + CuPa\beta$) + $CuPb$ (from which it diverges after some

distance). In other words, the correct homologization for the vein occurring between (M or MP +) CuA (+ CuPa α° *in part*) and AA1 is (CuPa α° *trans.* + CuPa α^*) + [(CuPa α^* + CuPa β) + CuPb].

From illustrations provided by TILLYARD (1925) and SHAROV (1968), the degree of vein fusions and translocations is variable in hind wings of the group. From the morphology exhibited by the forewing, and with respect to the putative ancestral state as exhibited in Permian orthopterans, I assume that CuPb and CuPa β are simple in hind wings of titanoptera.

I (BÉTHOUX 2005a) suggested that titanoptera and species assigned to the Linnaean family Geraridae are relatives on the basis of the following character states: in forewings, vein CuPa β branched; in hind-wings, vein CuPb branched. From the comparative analysis carried out above, CuPa β is simple in titanopteran forewings, and so is CuPb in hind wings. This hypothesis was based on an erroneous interpretation of titanopteran wing venation and is no longer supported. The lack of the character states 'in forewing, first posterior branch of CuPa α (CuPa α^*) occurring basal to the connection of CuPa α with CuA', and 'in the distal half of the forewing, RP and MA not fused', characteristic of the titanoptera (see below) but lacking in geraridaeans, support the view that both groups are not closely related: geraridaeans are stem-orthopterans, while titanoptera are nested within the taxon including orthopterans.

3.2. Systematic implications and taxonomic systems

Following his hypothesis of a close relationship between the family Geraridae and the order Titanoptera, and a Linnaean rank-based nomenclatural system, GOROCHOV (2001: 18) included the family Geraridae within the order Titanoptera and erected two suborders, Gerarina and Mesotitanida. He provided neither diagnosis nor formal definition that could allow assignment of species to these taxa. Additionally he mentions (p. 18) that "a less specialized, putative group of Gerarina, or collateral lineage, may be a possible ancestral group for the Mesotitanina and all other Orthopteroidea". In a collegial contribution RASNITSYN (2002) and GOROCHOV & RASNITSYN (2002) consider the family Geraridae as stem-'Polyneoptera', distinct from the order Mesotitanida, itself considered as equivalent to Titanoptera (BELAYEVA et al. 2002). As a result, one is puzzled with the sense to be given to the taxon name 'Titanoptera'. Additionally, the sub-order Mesotitanida are viewed by GOROCHOV (2001) and GOROCHOV & RASNITSYN (2002) as a paraphyletic group including stem-orthopterans. Ultimately GOROCHOV (2003, 2004) reiterates the use of the taxon name 'Titanoptera'.

Indeed, as suggested by SHAROV (1968, 1971), the order Titanoptera is closely related to taxa previously assigned to the subfamily Tcholmanvissiinae, itself included in the order Orthoptera. In other words the subfamily Orthoptera-Tcholmanvissiinae must include the order Titanoptera. Strictly following a rank-based approach would necessitate an in depth reorganization of corresponding taxa ranks.

In order to avoid issues inherent to the Linnaean approach I follow the taxonomic system the development of which is initiated in BÉTHOUX (2007d) and implemented in BÉTHOUX (2007e). For convenience, main aspects of this procedure are repeated herein. Each taxon definition is set up with the designation of two cladotypes that are specimens exhibiting a designated type-character-state. Cladotypes must belong to different species. A name designates a monophyletic group until one of the following assumptions is falsified: (1) the character state typified by cladotypes is homologous in cladotypic species, (2) the character state typified by cladotypes is derived, and (3) individuals exhibiting the type character state evolved from an isolated (segments of) metapopulation lineage. Taxa are assemblages for which monophyly is objectively defined, testable, and emendable.

For convenience, a taxonomic application consistent with the ICZN is provided in Appendix 1. The application is designed with the aim of maximizing the hierarchical content or names the suffix of which is associated to a rank. For that purpose, each supra-generic taxon is composed of only two taxa of inferior rank. This application retrieves the same phylogenetic information as the cladotypic application performed below (and see Appendix 3; the genus *Mesotitan* Tillyard, 1916 as newly understood might not be monophyletic), plus hierarchical information based on suffixes associated to ranks. This application is left with the problem of the authorship of the taxon name Titanoptera (see below).

Prior to the redefinition of taxa including the species previously assigned to the family Tcholmanvissiidae by BÉTHOUX & NEL (2002b) and to the order Titanoptera by SHAROV (1968) and GOROCHOV (2003), I take the opportunity of adapting a more inclusive taxon in which these species are nested. This should avoid mixing Linnaean and cladotypic taxon names further in the discussion. Provisional taxa compositions are provided in Appendices 2–3. Presumed hierarchy of taxa defined below is summarized on Fig. 3.

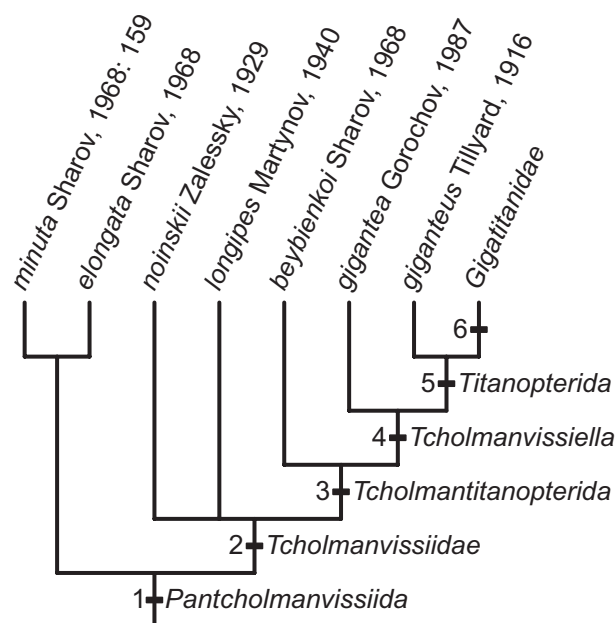


Fig. 3. Scheme of presumed hierarchy in *Pantcholmanvisiidae*; defining character-states (see text for abbreviations): 1: in forewing, first posterior branch of $CuPa\alpha$ ($CuPa\alpha'$) occurring basal to the connection of $CuPa\alpha$ with CuA ; 2: in the distal half of the forewing, RP and MA distinct from each other; 3: in forewing, $CuPa\beta$ and $CuPa\alpha'$ have the same point of origin from $CuPa\alpha$; 4: in forewing, at least one branches of $CuPa\alpha'$ has the same point of origin as $CuPa\alpha'$; 5: in forewing, $CuPa\alpha' + CuPa\beta$ and $CuPb$ have the same point of origin; 6: in forewing, $M + CuA$ separates into MA and $MP + CuA$.

Archaeorthoptera nom. Béthoux & Nel, 2002a, dis.-typ.n.

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in forewings, CuA (fused with M or diverging from it) connected to CuP or one of its branches’, as exhibited by *fisheri* Brongniart, 1885 and *schneideri* Béthoux, 2005c, has been acquired (venation designations as in BÉTHOUX & NEL 2002a).

Cladotypes. Specimens MNHN-DHT-R51164 (belonging to *fisheri* Brongniart, 1885; see BÉTHOUX & NEL 2002a: figs. 13–14; BÉTHOUX & NEL 2003: fig. 4) and ROM 45568 (holotype of *schneideri* Béthoux, 2005c; see BÉTHOUX 2005c: figs. 1–3).

Paracladotypes. Specimens MNHN-DHT-R51269 and MNHN-DHT-R51139 (belonging to *fisheri* Brongniart, 1885; see BÉTHOUX & NEL 2003: figs. 2, 3, respectively).

Discussion. The word ‘connected’ as used in the character formulation encompasses a short contact of the two veins to a long fusion. BÉTHOUX & NEL (2002a: 14) provided another character (state) formulation for one of the autapomorphies of the taxon *Archaeorthoptera* they list, referring to the same structure: “convex

CuA emerging from convex $M + CuA$ [...] distally fused with anterior branch ($CuPa$ or $CuPa\alpha$) of CuP ”. At the time BÉTHOUX & NEL (2002a) named the taxon *Archaeorthoptera*, all known species exhibiting a fusion of CuA (distal to its divergence from M) with CuP involved the anterior branch of the latter. A condition was identified which I considered as plesiomorphic in the species *dumasii* Brongniart, 1879, which exhibits, in hind wings, a brief connection of CuA with the stem of CuP , before the latter vein branches (BÉTHOUX 2003). It is clear that states regarding the branching pattern of CuP actually belong to different character(s) from those character states regarding the connection of CuA with CuP . The character (state) formulated by BÉTHOUX & NEL (2002a) includes two different characters.

The new formulation of the type-character-state is modified in order to avoid ambiguity and minimize the need of future emendations. The new formulation is not subsumed in the character (state) formulation of BÉTHOUX & NEL (2002a). The situation is rather opposite: the original character state necessarily occurs if the new character state occurs. Additionally these authors cannot be granted as the authors who first designated a single diagnostic character state of the taxon *Archaeorthoptera* because they list several autapomorphies in the diagnosis of the taxon. The taxon name *Archaeorthoptera* is then not preoccupied.

The putative ancestral state is ‘in forewings, CuA (fused with M or diverging from it) distinct from CuP ’. There is no argument in favour of the hypothesis of a convergent origin of the type-character-state among cladotypic species. This character state is assumed to be derived, although close adelphospecies and amittaspecies are unknown. At least the defining character state is absent in all other polyneopteran taxa. I assume that individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms.

The taxon *Archaeorthoptera* is nested within an unnamed taxon which type-character-state is ‘ CuA fuses with M at the wing base’. However, there is no direct evidence of this fusion (see BÉTHOUX & NEL 2002a; BÉTHOUX 2007a for support of this hypothesis). This taxon is not cladotypically defined because appropriate cladotypes are unknown. However, the fusion of CuA with M is implicit in the definition of the *Archaeorthoptera*.

The species *elongata* Brongniart, 1893: 433, listed in the composition list (see Appendix 2), is referred to as *Ctenoptilus elongatus* (Brongniart, 1893) by BÉTHOUX & NEL (2004). The authors coordinated the original specific epithet, *elongata*, according to a new generic attribution (according to the ICZN, articles 31.2, 34.2). There is no reason to follow this proce-

dure under cladotypic taxonomy, because it results in species name instability. The original specific epithet is then restored.

***Pantcholmanvissiida* nom.n., dis. Béthoux & Nel, 2002b, typ.n.**

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in forewing, first posterior branch of CuPa α (CuPa α ’) occurring basal to the connection of CuPa α with CuA’, as exhibited by *noinskii* Zalesky, 1929 and *beybienkoi* Sharov, 1968, has been acquired (venation designations as in BÉTHOUX & NEL 2002a; see also BÉTHOUX & NEL 2002b).

Cladotypes. Specimens PIN 3353/391 (holotype of *noinskii* Zalesky, 1929; see BÉTHOUX & NEL 2002b: fig. 6) and PIN 1700/4126 (holotype of *beybienkoi* Sharov, 1968; see BÉTHOUX & NEL 2002b: fig. 10).

Paracladotypes. Specimens PIN 117/258 & 259 and PIN 3353/381 (see BÉTHOUX & NEL 2002b: figs. 7, 8, respectively).

Derivatio nominis. Name based on the word ‘Tcholmanvissiidae’ and the prefix ‘Pan’, ‘all’ in Greek.

Discussion. The putative ancestral state is ‘in forewing, first posterior branch of CuPa α occurring distal to the connection with CuA’. The type-character-state is presumably synapomorphic for the *Pantcholmanvissiida* because it is absent in other *Archaeorthoptera*. There is no argument in favour of the hypothesis of a convergent origin of the type-character-state among cladotypic species. I assume that individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms. The *Pantcholmanvissiida* encompasses species assigned to the Linnaean family Tcholmanvissiidae by BÉTHOUX & NEL (2002b), as well as those belonging to the Linnaean order Titanoptera as understood by SHAROV (1968) (see also GOROCHOV 2003).

GOROCHOV (1995: 86) formulated a character (state) as a single synapomorphy of a group including his (Linnaean) sub-families Tettoedischiinae and Tcholmanvissiinae. Under the wing venation nomenclature used herein, GOROCHOV (1995) suggested that the branch basal to the fusion of CuA with CuPa α (indicated by * on Fig. 4) actually belongs to CuA + CuPa α , and fuses with CuPa α . His interpretation involves the same structure (CuPa α) as that involved in the definition of the *Pantcholmanvissiida*. The possibility that GOROCHOV (1995) should be granted as the first author who mentioned the type-character-state of the *Pantcholmanvissiida* must then be discussed. BÉTHOUX & NEL (2002b) argued that GOROCHOV (1995) interpretation is “hardly possible”, mainly because a branch of CuA

+ CuPa α cannot arise basal to the fusion of CuA with CuPa α . However, there are two scenarios that could fit with GOROCHOV’s (1995) statement.

First, CuPa α could be branched proximally and its anterior branch fused with M + CuA (Fig. 4A). The composite vein CuA + (anterior branch of) CuPa α would then diverge from M. It can be imagined that, in an unknown ‘primitive’ taxon, the first branch of CuA + CuPa α became successively oblique, then aligned with the posterior branch of CuPa α , resulting into the morphology exhibited by the *Pantcholmanvissiida*. However, there is a major impossibility in this scenario: CuPa α and its ‘sister-branch’ CuPa β are emitted from CuPa distal from the wing base (where the hypothetical branching of CuPa α and fusion with CuA could be unobservable on fossil material), and there is no known related taxon in which an anterior branch of CuPa α fuses with M + CuA distal to the origin of CuPa.

The second scenario is more elaborate (Fig. 4B). It implies that after its formation (i.e. fusion of CuA and CuPa α), CuA + CuPa α is bent backwards, branches, and finally runs towards the wing apex, following the same path as earlier. This would imply that the vein indicated herein as CuPa α ° is composed of {[CuPa α + (CuA + CuPa α)] + (CuA + CuPa α)}. This would be evidenced by a strengthening of the corresponding structure, which does not occur in the known species.

The homology I propose instead is that the vein indicated by * on Fig. 4 belongs to CuPa α (i.e. is CuPa α * as mentioned above) and arises before the anterior branch of the later (CuPa α °) fuses with CuA (Fig. 4C). It is assumed that the branch of CuPa α occurring basal to the fusion with CuA in *Pantcholmanvissiida* is homologous to the first branch of CuPa α that diverges from CuA + CuPa α (i.e. distal to the fusion of CuA with CuPa α) in sister-taxa of *Pantcholmanvissiida*. From the available data, this is a more plausible homology statement.

In summary, the homology statement provided by GOROCHOV (1995) can be seen as a correct primary homology statement within *Pantcholmanvissiida* (the character state is similar in species assigned to this taxon), a plausible secondary homology statement within *Archaeorthoptera* (the character state was acquired by common ancestry), but the primary homology statement is erroneous within *Archaeorthoptera* (the structure described as the character is not derived from the structure it is supposed to). However, the most important point is that, theoretically, the character (state) defined by GOROCHOV (1995) and the character state I use for defining the *Pantcholmanvissiida* could co-occur (Fig. 4D). This can be viewed as characters that fail the conjunction test (PATTERSON 1982, 1988; see also DE PINNA 1991), hence they are not homologous. Therefore GOROCHOV (1995) cannot be granted

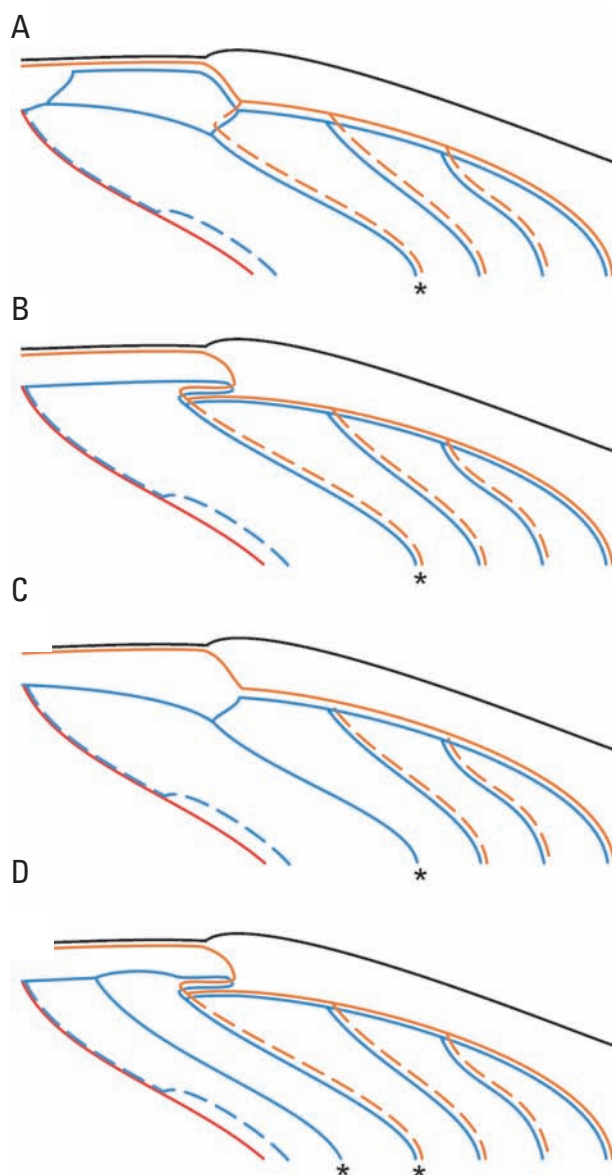


Fig. 4. Possible scenarios for the homologization of the vein indicated by *, either as a branch of CuA + CuPa α fused with CuPa α (GOROCHOV 1995) (A, B) or as a branch of CuPa α (BÉTHOUX & NEL 2002b) (C), and possible co-occurrence of homologizations B and C (D) (colour coding as in Fig. 1; posterior branches of CuA are represented by dashed lines as CuA is considered as branched by GOROCHOV 1987, 1995 but simple in this contribution; CuPa α is represented by a dashed line as it is not the focus of this illustration, and it is not fused with CuPa β in all Pantcholanvissiidae; see text for abbreviations). **A:** CuPa α is branched, its anterior branch fuses with M + CuA, and its posterior branch fuses with CuA + CuPa β . **B:** CuA + CuPa α , after its formation (fusion of CuA and CuPa α), bends backwards, branches, and finally runs towards wing apex. **C:** CuPa α is branched basal to its connection with CuA. **D:** co-occurrence of homologizations B and C.

as the author who first designated the type-character-state of the *Pantcholanvissiida* as defined herein, but BÉTHOUX & NEL (2002b), who listed the corresponding character state as the only diagnostic character of the family Tcholmanvissiidae.

The taxon name Tcholmanvissiidae cannot be used for the taxon under scrutiny because it is preoccupied, as SHAROV (1968) explicitly associated it to another character state (see below). Therefore, another name must be searched for. GOROCHOV (1995: 86) erected no name for the taxon including his Tettoedischiinae and Tcholmanvissiinae. Therefore I erect a new taxon name.

***Tcholmanvissiidae* nom. Zalesky, 1934,
dis. Sharov, 1968, typ.n.**

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in the distal half of the forewing, RP and MA distinct from each other’, as exhibited by *longipes* Martynov, 1940 and *giganteus* Tillyard, 1916, has been acquired.

Cladotypes. Specimens PIN 1700/1488 (holotype of *longipes* Martynov, 1940; see BÉTHOUX & NEL 2002b: fig. 6) and AM F.36274 (specimen attributed to *giganteus* Tillyard, 1916; see MCKEOWN 1937: figs. 1–3, pl. 4; see JELL 2004: unnumbered figure on p. 29; GRIMALDI & ENGEL 2005: fig. 7.42).

Paracladotypes. Specimens PIN 1452/5 and PIN 1700/1454 (belonging to *longipes* Martynov, 1940; see BÉTHOUX & NEL 2002b: figs. 2, 4, respectively), and MNH In. 37340 (belonging to *giganteus* Tillyard, 1916; Fig. 2A; see Zeuner, 1939: pl. LXXX, fig. 1).

Discussion. The putative ancestral state is ‘in the distal half of the forewing, RP and MA fused for some distance’. The type-character-state appeared more than once among Orthoptera (BÉTHOUX & NEL 2002a). It is a reversion of a character state acquired in stem-orthopterans, namely the fusion of RP with MA (or one of its anterior branches). A connection of RP with MA is present in successive sister-groups of the *Tcholmanvissiidae*. Considering the series of character state changes that separate the *Tcholmanvissiidae* from other orthopterans exhibiting the same character state, it is assumed that it appeared in the common ancestor of *longipes* and *andersoni* and is locally apomorphic. There is no argument in favour of the hypothesis of a convergent origin of the type-character-state among cladotypic species. I assume that individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms. This taxon encompasses the subfamily Tcholmanvissiinae as understood by BÉTHOUX & NEL (2002b) and the order Titanoptera as understood by SHAROV (1968).

Despite the fact that the name Tcholmanvissiidae has a suffix typical of Linnaean families, I adapt it unmodified in the new cladotypic taxonomy because it is preoccupied. Neither ZALESKY (1929), nor ZALESKY (1934), nor MARTYNOV (1940) mentioned a unique

character (state) diagnostic of the family Tcholmanvissiidae, but SHAROV (1968) mentioned that “the species of Tcholmanvissiidae differ from the Oedischidae mainly in the absence of an anastomosis between the anterior branch of MA and RS [RP]” (translation from SHAROV 1971: 29); he mentioned no other “main” diagnostic character state. This is a homology statement synonymous to that given for the type-character-state of *Tcholmanvissiidae* as herein, although under a different wing venation nomenclature. Therefore priority is given to SHAROV (1968) as the author who first designated the type-character-state of this taxon.

The holotype of the species *longipes* Martynov, 1940 is selected as cladotype because several forewings belonging to this species are described and they consistently exhibit an MA distinct from RP (see BÉTHOUX & NEL 2002b).

After BÉTHOUX & NEL (2002b), the genus *Tcholmanvissia* (erected by Zalesky, 1929) includes two species (*noinskii* Zalesky, 1929, and *longipes* Martynov 1940). In the diagnosis provided by these authors, not a single diagnostic character state that could have allowed the name ‘Tcholmanvissia’ to be adapted is mentioned. I found none in the literature. The taxon *Tcholmanvissiidae* is the least inclusive taxon including *noinskii* and *longipes* that is cladotypically defined, therefore it should be used as the taxonomic address (CANTINO et al. 1999; DAYRAT et al. 2004) for the species previously assigned to the genus *Tcholmanvissia*. Correct taxonomic combinations are then *Tcholmanvissiidae noinskii* Zalesky, 1929 and *Tcholmanvissiidae longipes* Martynov 1940.

There is some uncertainty regarding the specific assignment of the specimen AM F.36274, to which the status of cladotype is given in various places herein. Until the “argument” mentioned by JELL (2004: 8) is elucidated, I follow SHAROV (1968), CARPENTER (1992), and GOROCHOV & RASNITSYN (2002) who considered that it belongs to the species *giganteus* Tillyard, 1916. In any case, under cladotypic taxonomy, names of species and of taxa other than species are defined independently. A supra-specific taxon name definition can be emended if the specific identity of a cladotype provided in an early definition is incorrect. If so, the cladotype identity prevails over the species name given in the definition (BÉTHOUX 2007d).

***Tcholmantitanopterida* nom.-dis.-typ.n.**

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in forewing, CuPaβ and CuPaα’ have the same point of origin from CuPaα’, as exhibited by *gigantea* Gorochov, 1987 and *giganteus* Tillyard, 1916, has been acquired (venation designations as in BÉTHOUX & NEL 2002b and herein).

Cladotypes. Specimen PIN 3353/78 (holotype of *gigantea* Gorochov, 1987; see BÉTHOUX & NEL 2002b: fig. 11) and AM F.36274 (specimen attributed to *giganteus* Tillyard, 1916; see McKEOWN 1937: figs. 1–3, pl. 4; JELL 2004: unnumbered figure on p. 29; GRIMALDI & ENGEL 2005: fig. 7.42).

Derivatio nominis. Name based upon the words Tcholmanvissia and Titanopterida.

Discussion. The putative ancestral state is ‘in forewing, CuPaβ and CuPaα’ with distinct origins’. The type-character-state is presumably apomorphic of the *Tcholmantitanopterida* because it is absent in other *Archaeorthoptera*, *Pantcholmanvissiida*, and *Tcholmanvissiidae*. There is no argument in favour of the hypothesis of a convergent origin of the type-character-state among cladotypic species. I assume that individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms.

The genus *Jubilaeus* Sharov, 1968 includes the species *beybienkoi* only. As far as I am aware there is no single diagnostic character state that could allow its ‘association’ to another taxon within the *Tcholmantitanopterida*. The adaptation of the name ‘Jubilaeus’ into cladotypic taxonomy is then currently impossible. For the same reason as above, the correct taxonomic combination for this species is *Tcholmantitanopterida beybienkoi* Sharov, 1968.

***Tcholmanvissiella* nom. Gorochov, 1987, dis.-typ.n.**

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in forewing, at least one branch of CuPaα° has the same point of origin as CuPaα*’, as exhibited by *gigantea* Gorochov, 1987 and *giganteus* Tillyard, 1916, has been acquired (venation designations as in BÉTHOUX & NEL 2002a and herein).

Cladotypes. Specimens PIN 3353/78 (holotype of *gigantea* Gorochov, 1987; see BÉTHOUX & NEL 2002a: fig. 11) and AM F.36274 (specimen attributed to *giganteus* Tillyard, 1916; see McKEOWN 1937: figs. 1–3, pl. 4; JELL 2004: unnumbered figure on p. 29; GRIMALDI & ENGEL 2005: fig. 7.42).

Paracladotypes. Specimens NHM In. 37340 and NHM In. 37341 (specimens attributed to *giganteus* Tillyard, 1916; Fig. 2A,B, respectively; see ZEUNER 1939: pl. LXXX, figs. 1, 2, respectively).

Discussion. The putative ancestral state is ‘in forewing, all branches of CuPaα° have a point of origin distinct from that of CuPaα*’. The type-character-state is presumably apomorphic of the *Tcholmanvissiella* because it is absent in other *Archaeorthoptera*, *Pantcholmanvissiida*, *Tcholmanvissiidae*, and *Tcholmantitanopterida*. There is no argument in favour of the hypothesis of a convergent origin of the type-charac-

ter-state among cladotypic species. I assume that individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms.

GOROCHOV (1987: 79) provided a diagnosis of the genus *Tcholmanvissiella* which is: “on forewing, the stem of MP + CuA1 [CuA + CuPα°] has almost no branches, and main ridge of branches of MP + CuA1 [CuA + CuPα°] is located proximally to anastomosis of MP [CuA] with CuA1 [CuPα°]”. Once again, it is difficult to understand how branches of CuA + CuPα° could occur proximal to the fusion of the constituents of this composite vein (CuA and CuPα°). If one considers GOROCHOV’s (1987) diagnosis as composed of a single character state (but see below), this character state is distinct from that used to define the *Tcholmanvissiella* as herein: for the same reasons as detailed above (see discussion on *Pantchomanvissiida*), the character states ‘main ridge of branches of CuA + CuPα° located proximally to anastomosis of CuA with CuPα°’ could co-occur with the character state ‘in forewing, at least one branches of CuPα° has the same point of origin as CuPα*’. Therefore GOROCHOV (1987) cannot be granted as the first author who designated the type-character-state of the taxon *Tcholmanvissiella* as defined herein.

If one considers GOROCHOV’s (1987) diagnosis as composed on a single character state, the taxon name *Tcholmanvissiella* is preoccupied. However, there is no argument supporting this view. In the same paper, several diagnoses in which distinct characters (states) are listed end with “, and [last character state]”. Therefore, in “the stem of MP + CuA1 [CuA + CuPα°] has almost no branches, and main ridge of branches of MP + CuA1 [CuA + CuPα°] is located proximally to anastomosis of MP [CuA] with CuA1 [CuPα°]”, “main ridge of branches of MP + CuA1 [CuA + CuPα°] is located proximally to anastomosis of MP [CuA] with CuA1 [CuPα°]” appears as a second character (state) distinct from the former. Therefore, I suppose that GOROCHOV’s (1987) diagnosis refers to two different characters (states), and that the name *Tcholmanvissiella* is not preoccupied. Hence I can freely adapt it in cladotypic taxonomy.

The only species assigned by GOROCHOV (1987) to the genus *Tcholmanvissiella* has no known diagnostic character state on its own, and cannot be associated to any known species apart from those assigned to the *Titanopterida* (defined below). In other words, this species is the only member of the *Tcholmanvissiella* that is not a *Titanopterida*. The least inclusive taxon including *gigantea* that is cladotypically defined is *Tcholmanvissiella*. Incidentally the Linnaean binomial is preserved: the correct combination is *Tcholmanvissiella gigantea* Gorochoy, 1987.

One could have noticed that cladotypes of taxa *Tcholmantitanopterida* and *Tcholmanvissiella* are iden-

tical. It is not an issue under the taxonomic procedure used herein because typification is based upon a pair of individuals *and* a character state (BÉTHOUX 2007d).

Titanopterida nom.-dis.-typ.n.

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in forewing, CuPα* + CuPαβ and CuPb having the same point of origin’, as exhibited by *giganteus* Tillyard, 1916 and *vulgaris* Sharov, 1968, has been acquired (venation designations as in BÉTHOUX & NEL 2002a and herein).

Cladotypes. Specimens AM F.36274 (specimen attributed to *giganteus* Tillyard, 1916; see McKEOWN 1937: figs. 1–3, pl. 4; JELL 2004: unnumbered figure on p. 29; GRIMALDI & ENGEL 2005: fig. 7.42) and PIN 2240/4593 (holotype of *vulgaris* Sharov, 1968; see SHAROV 1968: fig. 50B).

Derivatio nominis. Based on the word ‘Titanoptera’.

Discussion. The putative ancestral state is ‘in forewing, CuPα* + CuPαβ and CuPb having distinct points of origin’. The type-character-state is presumably apomorphic of the *Titanopterida* because it is absent in other *Archaeorthoptera*, *Pantchomanvissiida*, *Tcholmanvissiidae*, *Tcholmantitanopterida*, and *Tcholmanvissiella*. I assume that cohesion mechanisms isolated individuals exhibiting the type-character-state from those that do not. The occurrence of the type-character-state on the specimen PIN 2240/4593 was assessed based upon examination of photographs provided by A.P. Rasnitsyn (pers. comm. 2007).

Adaptation of a name for this taxon is a tricky case. The composition of the taxon matches that given by SHAROV (1968: 123) to the order Titanoptera. This author (p. 123) mentioned two character states that differentiate the order Titanoptera from the order Orthoptera, and none are formulated precisely enough to be eligible as type-character-state. Indeed, SHAROV (1968) is not the author of this taxon name, but BRONGNIART (1885: 379), who erected it as a genus name for a fragmentary fossil specimen I regard as belonging to stem-odonatans. BRONGNIART (1885) did not explicitly associate this name to a single character state.

TILLYARD (1916) first described a species belonging to the order Titanoptera as understood by SHAROV (1968). He assigned it to a new genus, *Mesotitan*, but did not provide a single diagnostic character (state), nor any state convincingly diagnostic. Later on TILLYARD (1925) described a new species (which is actually a hind wing of the former species) he assigned to the same genus *Mesotitan*, and erected the family Mesotitanidae. However, none of the character states he mentioned are strictly diagnostic of the taxa he created. In the same vein CRAMPTON (1928) erected the order Mesotitanoptera on the basis of the family

name Mesotitanidae without providing any diagnosis.

Although they state that the names Mesotitanida (first coined by GOROCHOV 2001 as that of an order synonym of Gerarida) and Titanoptera refer to the same taxa, GOROCHOV & RASNITSYN (2002) preferred the former, and refer to TILLYARD (1925) as the person who erected the former name. However, this is not the case: this reference is based on a rule-free coordination of a Linnaean familial name [as it is, Mesotitanidae, erected by TILLYARD (1925)] into a Linnaean ordinal name, and following a rule of priority (TILLYARD 1925 rather than SHAROV 1968). This procedure is not followed here. Neither GOROCHOV (2001) nor GOROCHOV & RASNITSYN (2002) provided a unique character state diagnostic of the order Mesotitanida. GOROCHOV (2001) also erected the subordinal name Mesotitanina, without mention of a single diagnostic character state.

Therefore, as far as I am aware, there is no previous association of a single character state to a taxon name including the species assigned to the order Titanoptera by SHAROV (1968). All available Linnaean names refer to the great size of most known species, but this is hardly a reliable character for defining a taxon. Additionally, the situation with names erected under the Linnaean system is confusing. Therefore, I erect a new name, designate a new type-character-state, and designate cladotypes accordingly.

Regarding the composition of the group, the position of the species *vladimiri* Gorochov, 2004 (assigned to the Linnaean genus *Permotitan* Gorochov, 2004) must be discussed. An anomaly of the hypothesis stating that the geraridaeans and titanopterans are close relatives, defended by GOROCHOV (2001) and followed by BÉTHOUX (2005a), was the absence of both groups during the whole Permian period. This was before GOROCHOV (2004) assigned *vladimiri*, from the Permian Vorkuta coal basin (Russia), to the order Titanoptera, or closely related to this taxon. This assignment was based upon (1) the large size of the specimen (estimated forewing length about 140 mm), (2) the occurrence of regular cross-venation between ScP branches, and (3) the area between the anterior wing margin and ScP that does almost not taper proximal to its end. Size (1) can hardly be viewed as a character of definitive phylogenetic interest. Character (2) is not an obvious trait of *Titanopterida* as it is not occurring in *libelluloides* Sharov, 1968. This character varies greatly among Permian orthopterans and occurs in many *Archaeorthoptera*. The validity of the character (3) is difficult to assess in *Titanopterida* yielded by the deposit of Madygen (Trias; Russia) because of the effect of post-depositional deformation that affected fossils (SHAROV 1968; RASNITSYN 1982). Unfortunately, this material is the basis for most of our knowledge on *Titanopterida*. SHAROV (1971: 210) described specimens

probably belonging to the species *extensus* Sharov, 1968 as having a “costal field gradually tapering to the apex of the wing”, suggesting that character (3) is either difficult to appreciate or not diagnostic of *Titanopterida*, or both.

Additionally *vladimiri* exhibits ScP branches making a 40° angle with the main stem of ScP. When present in *Titanopterida*, such branches usually make a more oblique angle in forewing, especially in the distal area. Additionally, the point of divergence of MA and MP (free part of MP under the nomenclature used by Gorochov) is located in a very distal position, unlike in known *Tcholmanvissiidae*. Finally, it must be noticed that the restoration of *vladimiri* provided by GOROCHOV (2004), based upon a very incomplete and single specimen, is highly speculative. It cannot be ruled out that a fusion of the anterior branch of MA with RP, commonplace among Permian orthopterans but absent in *Tcholmanvissiidae*, actually occurred in this species. Finally, critical review of data on *vladimiri* lead me to conclude that it cannot be conclusively assigned to the *Pantcholmanvissiida*.

***Gigatitanidae* nom. Sharov, 1968, dis.-typ.n.**

Definition. Species that evolved from the (segments of) metapopulation lineage in which the character state ‘in forewing, M + CuA separates into MA and MP + CuA’, as exhibited by *vulgaris* Sharov, 1968 and *extensus* Sharov, 1968, has been acquired (venation designations as in BÉTHOUX & NEL 2002a).

Cladotypes. PIN 2240/4593 (holotype of *vulgaris* Sharov, 1968; see SHAROV 1968: fig. 50B) and PIN 2240/4503 (paratype of *extensus* Sharov, 1968).

Paracladotypes. Specimens PIN 2240/4526 and PIN 2555/1541 (see SHAROV 1968: pl. XII figs. 2 and 5, respectively), and FG/596/IV/1 (see Figs. 5–6), all attributed to *vulgaris* Sharov, 1968.

Discussion. The putative ancestral state is ‘in forewing, M + CuA separates into M (= MA + MP) and CuA’. The type-character-state is present in *grylliformis* Sharov, 1968, which is a genuine cricket. The type-character-state is presumably apomorphic of the *Gigatitanidae* because it is absent in other *Pantcholmanvissiida*, *Tcholmanvissiidae*, *Tcholmantitanopterida*, *Tcholmanvissiella*, and *Titanopterida*, all taxa from which *grylliformis* Sharov, 1968 can be readily excluded. I assume that individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms. The occurrence of the type-character-state on specimens PIN 2240/4593 and PIN 2240/4503 was assessed after examination of photographs provided by A.P. Rasnitsyn (pers. comm., 2007)

SHAROV (1968: 131) mentioned the selected type-

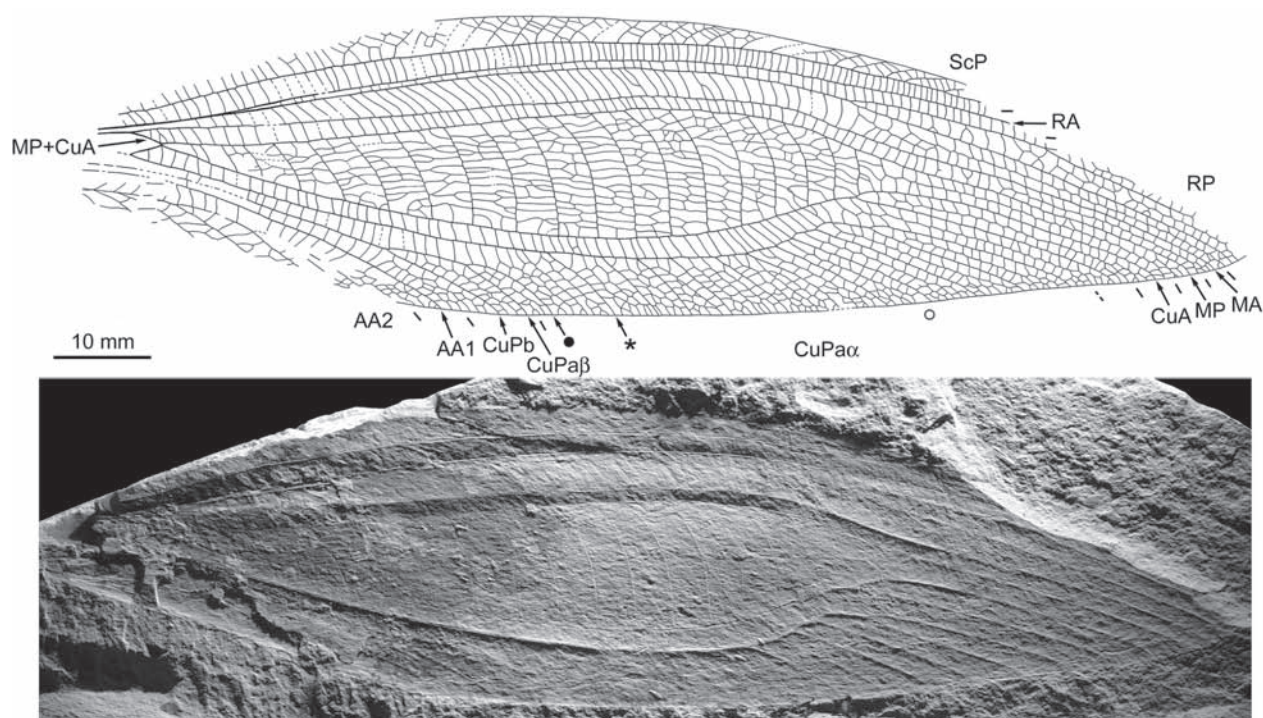


Fig. 5. Specimen FG 596/IV-1, assigned to *vulgaris* Sharov, 1968, paracladotype of *Gigatitanidae* nom. Sharov, 1968, *dis.-typ. n.*: drawing of the venation and photograph (negative imprint of a right forewing, reversed; see text for abbreviations).

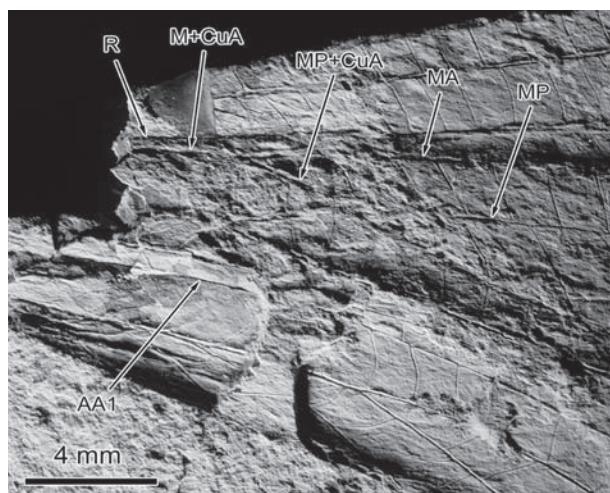


Fig. 6. Specimen FG 596/IV-1, assigned to *vulgaris* Sharov, 1968, paracladotype of *Gigatitanidae* nom. Sharov, 1968, *dis.-typ. n.*: detail of the wing base (negative imprint of a right forewing, reversed, light-mirrored; see text for abbreviations).

character-state as one of the diagnostic character (state) of the family Gigatitanidae: “the base of MA_2 [MP] is displaced to MP [CuA] or even to MP + CuA_1 [CuA + $CuPa\alpha^\circ$]”. The character state is not mentioned in the determination key provided by SHAROV (1968: 157), where he cited two characters (states). Hence there is no known preoccupation of the name. My decision regarding the choice of the character-state is based upon my opinion that it can be more sharply defined than other characters mentioned by Sharov, hence minimizing the risk of future emendations.

SHAROV (1968: 202) distinguished the genus *Nanotitan* Sharov, 1968, to which he assigned *extensus*, from the genus *Gigatitan* Sharov, 1968, to which he

assigned *vulgaris*, based upon the following characters (states): “absence of a differentiated proximal branch of Sc [ScP], [...] fusion of the base of MA_2 [MP] and MP + CuA_1 [CuA], [...] and fusion of the bases of CuA_2 [$CuPa\alpha^\circ$ *trans.* + $CuPa\alpha^*$] and CuP [($CuPa\alpha^*$ + $CuPa\beta$) + CuPb]”. Although *extensus* is known from few specimens, all these characters suggest that they belong to a species distinct from *vulgaris*.

4. Discussion

4.1. Origin and evolution of the Titanopterida

Based on a new comparative analysis and interpretation, the wing venation pattern of the titanopterans / titanopteridans is homologised with respect that of other orthopterans / archaeorthopterans. The evolutionary history of the former group is then less puzzling than previously thought: rather than suddenly radiating and disappearing during the Triassic, *Titanopterida* arose from a set of large-sized Permian orthopterans. This scenario implies that raptorial forelegs, known in Triassic *Titanopterida* (SHAROV 1968), were acquired in orthopterans, and questions the view that ancestral orthopterans were herbivorous. Orthopterans gain an additional and unique stridulatory apparatus, occurring in both sexes, and *Titanopterida* experienced a reduction or loss of hind leg structures related to jump (SHAROV 1968). As now known the *Pantcholanvisiida* represents a lineage that survived the Permian / Triassic biocrisis. However an accurate estimation of the impact of this event on the taxon diversity is out-of-reach, due to the incompleteness of our record.

4.2. Fossil taxa and saturated morphologies

The paper highlights the contribution of fossil material for assessing homologies in derived taxa. The species *gigantea* Gorochoy, 1987 exhibits a fusion of $\text{CuPa}\alpha^*$ with $\text{CuPa}\beta$, which is an apomorphic state among orthopterans, but no translocation of $\text{CuPa}\alpha^0$ branches onto $\text{CuPa}\alpha^*$, a plesiomorphy within *Tcholmanvisiella*, to which it belongs. This interpretation resulted into a new homologization of the wing venation of *Titanopterida*, itself resulting into a strong support for one of the available phylogenetic hypotheses regarding the origin of the group.

It is worth mentioning that SHAROV (1968, 1971), despite his visionary statement that *Titanopterida* derived from *Tcholmanvisiidae*, did not achieve a correct homologization. In my opinion, this is arguably related to the fact that *gigantea* Gorochoy, 1987, with its unique character states combination, was unknown to him. Although this study concerns fossil taxa only, I consider this example as a demonstration of the usefulness of fossils for determining primary homologies and character states polarity, hence relationships, among taxa exhibiting saturated morphologies.

4.3. Practical cases of cladotypic taxonomy

This first application of cladotypic taxonomy unveiled several practical aspects of this nomenclatural system.

In the following section I discuss a proposition governing the adaptation of previously erected taxon names based on various cases of character state formulations, the issue of the occurrence of Linnaean suffixes within a cladotypic taxonomy, the issue of Linnaean binominals within a cladotypic taxonomy, and the capacity to handle the ancestor ‘species’ vs. apomorphy-less sister-species issue by the various nomenclatural systems. First, I discuss the question of accuracy of type character state formulations.

4.3.1. Character state formulations and antonyms

Formulation of type character states is a matter of semantics when coming to emendation of previous definitions. Although cladotypic taxonomy has the essential advantage of allowing definition emendations to be performed thanks to reference to type-specimens (BÉTHOUX 2007d), formulations should avoid polysemic words, so that the risk of confusion in future emendations is lowered. I suggest that antonyms could be mentioned in the discussion associated to the definition, or in the formulation even. The formulation of the putative ancestral state, which should be an antonym of the type character state formulation, fits these requirements. This mention is desirable as it could help to circumvent the meaning of the definition. Explicit references to figures are also desirable, as they are character state ostentations.

4.3.2. Adaptation and character state formulation

Earlier I insisted on the fact that a “taxon [...] name [...] is to be permanently anchored to the original homology assumption” (BÉTHOUX 2007d). It results in the notion of name pre-occupation, which can be applied to previously erected Linnaean taxa. Therefore the capacity to determine whether a former character state formulation includes, equates to, or is subsumed into a later character state formulation is essential for the adaptation of previously erected Linnaean names, as well as for emendation of cladotypically defined taxa. Three cases are possible: (1) a latter character state formulation is subsumed in a former one if the latter character state necessarily occurs if the former character state occurs, but not reciprocally; (2) a former character state formulation is equivalent to a latter one if the latter character state necessarily occurs if the former character state occurs, and reciprocally (i.e. the former character state necessarily occurs if the latter character state occurs); and (3) a latter character state formulation subsumes a former one if the former character state necessarily occurs if the latter character state occurs, but not reciprocally. In other words, (1) the latter character state formulation is a hyponym of the former character state formulation; (2) the latter

character state formulation is a synonym of the former character state formulation; and (3) the latter character state formulation is a hypernym of the former character state formulation. This test can be viewed as a derivation of the conjunction test (PATTERSON 1982, 1988; see also DE PINNA 1991). Adaptation of a preoccupied erected name explicitly related to a single diagnostic character state is possible in the second case only. Emendation of a previous taxon definition is acceptable only in the first case. If a previously erected Linnaean name is associated to a character state which is actually composed of several character states (e.g. Archaeorthoptera in BÉTHOUX & NEL 2002a), emendation is impossible because cladotypes are not available (see BÉTHOUX 2007d for emendation procedure). As a result, the taxon name is not preoccupied.

4.3.3. Preoccupation and Linnaean suffixes

Taxa for which names end with a Linnaean suffix could be preoccupied. This is the case of the taxon *Tcholmanvissiidae*, for which a previous author explicitly associated the corresponding taxon to a single character state. Two options are possible: either the taxon name is adapted unchanged, or a new name is created, considering that the previous one was not erected under cladotypic taxonomy. If one desires the work of previous researchers to be acknowledged, the former option is to be preferred. It must be noticed that the name of the type-genus of a given family could alternatively be selected. However, it is possible that both names are preoccupied, based on different diagnostic character states (as well as names of the corresponding subfamily, tribe, subtribe, etc., all derived from the genus name). Therefore, I suggest that Linnaean names to which a suffix has been assigned could be adapted unchanged under cladotypic taxonomy.

If so, and as a result of the adaptation process, a taxon, the name of which ends with a given Linnaean suffix, could include taxa for which names end with the suffix of an equivalent or higher rank. This is the case of the taxon *Tcholmanvissiidae*, including the taxon *Gigatitanidae*. In first instance this is confusing for taxonomic practitioners used to Linnaean ranks. However, this case happens when any Linnaean ranked taxon is found to be paraphyletic (which is the case of the family *Tcholmanvissiidae*). The treatment of this problem is merely different under Linnaean and cladotypic taxonomies: under the former, suffixes of taxon names are modified according the modification of their rank; under the latter, no modification is necessary, which I believe is to be preferred, as it renders taxonomy more stable. All in all, the occurrence of rank-based suffixes within a cladotypic taxonomy can be viewed as a legacy of the Linnaean framework, but some might prefer to strictly exclude corresponding names.

4.3.4. Linnaean binominals, taxonomic addresses, and preoccupation

Under rank-less uninominal species nomenclature, taxon names listed in a taxonomic address have the function of providing information about phylogenetic relationships of species (LANHAM 1965; CANTINO et al. 1999; DAYRAT et al. 2004): names of taxa of various inclusiveness precede the specific epithet (e.g. *Archaeorthoptera Pantcholmanvissiida Tcholmanvissiidae longipes* Martynov, 1940). If a Linnaean genus name is adapted, species belonging to this genus could be designated by the same combination as under Linnaean nomenclatural system (e.g. *Tcholmanvissiella gigantea* Gorochoy, 1987). It implies that the adaptation of taxon names previously understood as those of genera is critical if one's desire it to preserve continuity between Linnaean taxonomy and a new cladotypic one.

However, as a result of an expectable improvement of phylogenetic relationships resolution within Linnaean genera as currently understood, it is likely that new taxa nested 'between' adapted Linnaean genera and species will be defined. The rule stating that the taxonomic address of a species should end with the name of the least inclusive taxon implies that Linnaean binominals, as we now know them, will be lost at some point (but see below). This will result in discontinuity between a Linnaean and a mature cladotypic taxonomy. Nevertheless, it must be acknowledged that under the Linnaean nomenclatural system, new information on intra-generic relationships are taken into account by authoritatively and arbitrarily modifying the composition of the previous genus, authoritatively and arbitrarily erecting new genera, and, if necessary, modifying the specific epithet in accordance with the gender of the new genus to which a species is assigned (and, if necessary, authoritatively and arbitrarily modifying higher taxa ranks, hence their name). If the concern is about a stable binominals database, the Linnaean generic nomenclatural system is *not* more stable than a (least inclusive taxon name + uninominal) cladotypic system.

Still, if one's opinion is that authoritative and arbitrary selection of a name to be applied as 'pre-epithet' before a species 'epithet' would guarantee stability of a species database and allow an easier use of it, it can be envisioned that one of the taxon names of a species taxonomic address could be selected as a main 'pre-epithet'. However, I believe that the cladotypic procedure, coupled with the rank-less uninominal species proposition (LANHAM 1965; DAYRAT et al. 2004), is governed by quite intuitive principles. After all, a mature cladotypic taxonomy is, in a simplistic view, no less than a determination key in which dichotomies leave the choice between a (hypothetical) plesiomorphy and an (hypothetical) synapomorphy, each step

being preceded by modifications that arose earlier in the history of a taxon. This applies up to the species level, for which diagnoses could be provided (see BÉTHOUX 2007d for the species definition). Therefore a mature cladotypic taxonomy would be highly practical to taxonomy users, besides the crucial introduction of the concepts of biological evolution (through evidence of historical modification of character states) and of derived character state (rather than similarity) to non-professionals.

The rule of priority given to preoccupied names is in conflict with a possible rule of priority given to previous Linnaean genera (aimed at preserving Linnaean binominals). My opinion is that the former takes precedence over the latter, as I allocate more importance to the author who first identified a unique diagnostic character state of a taxon rather than to the author who first erected a name and authoritatively and arbitrarily (or by allegiance to one of the International Codes of Nomenclature) assigned it as genus name to a species.

4.3.5. Ancestor 'species' or apomorphy-less sister-species

The new nomenclatural system has the capacity to classify species that have no known apomorphy on their own but that of the least inclusive taxon to which they belong (e.g. *Tcholmanvissiella gigantea* Gorochoy, 1987). These 'species' are putatively composed of individuals belonging to the 'ancestor lineage', or are apomorphy-less sister-species of the other member of the taxon they belong to (in our example, the taxon *Titanopterida*). Cladotypic taxonomy relies on the assumption that *cohesion mechanisms isolated individuals exhibiting a type-character-state from those that do not, or individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms*. This is the null hypothesis. In our example, individuals of the taxon *Titanopterida* are supposed to have been isolated from those belonging to *Tcholmanvissiella gigantea* Gorochoy, 1987. Therefore, the latter taxon is automatically assumed to be an apomorphy-less (or 'apomorphy-unknown') sister-species rather than an ancestral species. If one proves that no isolation occurred between individuals that acquired the type-character-state of the *Titanopterida* and those belonging to *Tcholmanvissiella gigantea* Gorochoy, 1987, the isolation assumption is not respected, the former taxon is invalidated, and the latter taxon is a stem-lineage 'species' indeed. Several approaches exist that could demonstrate the absence of isolation (see DAYRAT 2005; and references therein). Nevertheless, in my opinion, the distinction between stem-lineage 'species' (or ancestor 'species') and apomorphy-less

sister-species is a question that has little practical implications on taxonomy. If palaeontological research is aiming at unveiling unknown character state combinations and providing data on the minimal divergence dates, cladotypic taxonomy is fully capable of dealing with these two main inputs: species name combinations convey phylogenetic information at the highest degree of precision, and the minimal age of a taxon is automatically that of its apomorphy-less sister-species: by definition, if this species is indeed an ancestral 'species', the taxon does not exist.

The Linnaean nomenclatural system necessitates the creation of a surfeit of ranked taxa for ancestral 'species' / apomorphy-less sister-species. The PhyloCode, as currently developed, is unable to deal with the question because it does not take into account the species case, this being due to the fact that it lacks the isolation assumption. With respect to these nomenclatural systems, the cladotypic one arguably handles the question in the most simple and informative way.

5. Conclusion

Comparative investigations carried out in this contribution demonstrate that the Triassic *Titanopterida* derived from Early Permian *Pantcholmanvissida*. Our view of titanopteridans evolution is greatly modified once the earlier relatives are taken into account: rather than suddenly radiating and disappearing during the Triassic, titanopteridans existed for at least 50 My (million years). Our poor record of this group does not allow any accurate estimation of the impact of the Permian / Triassic biocrisis on the group.

Forewing venation patterns are found to be highly complex, hence phylogenetically informative. I argue that more facilities should be involved in comparative morphological studies dedicated to the wing venation character system of palaeopteran and polyneopteran taxa, including extant ones. Putative results encompass improvement of the resolution of pterygotan phylogeny, rigorous definition of extinct and modern groups, altogether resulting in an improved knowledge of the early evolution of a taxon that represents more than half of the extant biodiversity, namely the winged insect.

Regarding the use of cladotypic taxonomy, avoiding mandatory ranks is found to be particularly relevant for fossil taxa, which endlessly exhibit original character state combinations informing us of the historical order of additive modifications that led to modern taxa. All these 'intermediate' taxa simply do not fit within a strictly ranked taxonomy, essentially based on modern taxa, themselves assumed to be of high rank. Based upon the practical case investigated in this

contribution, I see no particular aspect for which the nomenclatural system as governed by the PhyloCode (CANTINO & DE QUEIROZ 2006), a topology-based system (SERENO 2005), and the Linnaean one, overcome the cladotypic approach. Importantly, the cladotypic nomenclatural system deals with ‘ancestral’ species / apomorphy-less sister-species, comparatively in the simplest way.

It is clear that a code will have to be developed if cladotypic taxonomy becomes accepted and used. Current International Codes of Nomenclature provide a suitable pre-existing framework for holotypes and cladotypes designation and curation, and regarding starting dates for taxon names priority, among other aspects. Rules governing the adaptation of preoccupied names could be inspired from those governing names conversion in the PhyloCode. It is clear however that some practice will be necessary before all the aspects of cladotypic taxonomy will be unveiled, and a suitable code developed.

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8. Appendices

Appendix 1

Taxonomic treatment in accordance to the ICZN

Taxon Archaeorthoptera Béthoux & Nel, 2002b

Sub-order Titanoptera Brongniart, 1885 / Titanoptera Sharov, 1968 ?

Super-family Tettoedischioidea Gorochov, 1987

Family Tettoedischiidae Gorochov, 1987

Subfamily Tettoedischiinae Gorochov, 1987

Genus *Tettoedischia* Sharov, 1968

Tettoedischia minuta Sharov, 1968

Tettoedischia elongata (Sharov, 1968) comb.n.

Super-family Tcholmanvissioidea Zalesky, 1934

Family Tcholmanvissiidae Zalesky, 1934

Genus *Tcholmanvissia* Zalesky, 1929

Tcholmanvissia noinskii Zalesky, 1929

Tcholmanvissia longipes (Martynov, 1940)

Family Mesotitanidae Tillyard, 1925

Sub-family Jubilaeinae subfam. n. (type-genus: *Jubilaeus* Sharov, 1968)

Genus *Jubilaeus* Sharov, 1968

Jubilaeus beybienkoi Sharov, 1968

Sub-family Mesotitaninae Tillyard, 1925

Tribe Tcholmanvissiellini trib. n. (type-genus: *Tcholmanvissiella* Gorochov, 1987)

Genus *Tcholmanvissiella* Gorochov, 1987

Tcholmanvissiella gigantea Gorochov, 1987

Tribe Mesotitanini Tillyard, 1925

Genus *Mesotitan* Tillyard, 1916

Mesotitan giganteus Tillyard, 1916

Mesotitan libelluloides (Sharov, 1968) comb.n.

Mesotitan ovalis (Sharov, 1968) comb.n.

Mesotitan primitivus (Sharov, 1968) comb.n.

Mesotitan superior (Sharov, 1968) comb.n.

Genus *Gigatitan* Sharov, 1968

Gigatitan vulgaris Sharov, 1968

Gigatitan extensus (Sharov, 1968) comb.n.

Gigatitan magnificus (Sharov, 1968) comb.n.

Appendix 2

Provisional taxa composition of Archaeorthoptera

Archaeorthoptera nom. Béthoux & Nel, 2002b, dis.-typ.n.: all species assigned to the Linnaean taxa Orthoptera (see EADES et al. 2007; including the cladotypic taxon Pantcholanvissiida), Caloneurodea (species listed in BÉTHOUX et al. 2004 and RASNITSYN et al. 2004), Cnemidolestodea (Linnaean genera listed in BÉTHOUX 2005a; see also BÉTHOUX 2007b), and:

carbonis Handlirsch, 1904: 16 (see BÉTHOUX & NEL 2004, 2005)

carpentieri Pruvost, 1919 (see BÉTHOUX 2007c)

cubitalis Handlirsch, 1911 (see BÉTHOUX 2005c)

dumasii Brongniart, 1879 (see BÉTHOUX 2003)

elongata Brongniart, 1893: 433 (see BÉTHOUX & NEL 2004, 2005)

fischeri Brongniart, 1885 (see BÉTHOUX & NEL 2003)

lecrivaini Pruvost, 1919 (see LAURENTIAUX & LAURENTIAUX-VIEIRA 1980)

limburgica Pruvost, 1927 (see BÉTHOUX & NEL 2002a, KUKALOVÁ 1958)

macroptera van Beneden & Coemans, 1867 (see BÉTHOUX & NEL 2004, 2005)

mazonus Béthoux, 2005c

mirificus Carpenter & Richardson, 1971

onzii Pinto, 1990

palmiformis Bolton, 1922 (see BÉTHOUX & NEL 2004, 2005)

radialis Handlirsch, 1911 (see BURNHAM 1983)

ramosa Béthoux & Nel 2004

robusta Brongniart, 1893: 431 (see BÉTHOUX & NEL 2004, 2005)

rochacamposi Pinto & Pinto de Ornellas, 1978

ruhrensis Brauckmann & Koch, 1982 (see BRAUCKMANN et al. 1985)

sanguinettiae Pinto & Adami-Rodrigues, 1995

schneideri Béthoux, 2005c

splilopterus Handlirsch, 1911 (see BÉTHOUX 2006)

sylvatica Laurentiaux & Laurentiaux-Vieira, 1980

trecwithiensis Kukalová-Peck & Brauckmann, 1992 (see BÉTHOUX & NEL 2002a; BRAUCKMANN & HERD 2005)

vetus Scudder, 1885 (see BURNHAM 1983)

zeilleri Langiaux & Parriat, 1974

Species of uncertain validity:

- *martinsnetoi* Pinto in Würdig et al., 1998, *velizensis* Pinto & Pinto de Ornellas, 1981, *amosi* Pinto, 1992, *kurtzi* Pinto, 1980, all probable synonyms of *rochacamposi* Pinto & Pinto de Ornellas, 1978
- *ornellasae* Pinto, 1996, a probable hind wing of *rochacamposi* Pinto & Pinto de Ornellas, 1978
- *danielsi* Handlirsch, 1906, *rossae* Richardson, 1956, *collaris* Handlirsch 1911, *validum* Scudder, 1885, all probable synonyms of *vetus* Scudder, 1885

Appendix 3

Provisional taxa composition of Pantcholmanvissiida

***Pantcholmanvissiida* nom.n., dis. Béthoux & Nel, 2002a, typ.n.:** all species assigned to the *Tcholmanvissiidae* (see below), and:

elongata Sharov, 1968

minuta Sharov, 1968: 159

***Tcholmanvissiidae* nom. Zalessky, 1934, dis. Sharov, 1968, typ.n.:** all species assigned to the *Tcholmantitanopterida* (see below), and:

longipes Martynov, 1940

noinskii Zalessky, 1929

***Tcholmantitanopterida* nom.-dis.-typ.n.:** species assigned to the *Tcholmanvissiella* (see below), and:
beybienkoi Sharov, 1968

***Tcholmanvissiella* nom. Gorochov, 1987, dis.-typ.n.:** species assigned to the *Titanopterida* (see below) and:

gigantea Gorochov, 1987

***Titanopterida* nom.-dis.-typ.n.:** species assigned to the *Gigatitanidae* (see below) and:

giganteus Tillyard, 1916

libelluloides Sharov, 1968

ovalis Sharov, 1968

primitivus Sharov, 1968

superior Sharov, 1968

Species of uncertain validity:

- *tillyardi* Sharov, 1968, and *similis* Sharov, 1968: 197 (see also GOROCHOV 2003), all probable synonyms of *primitivus* Sharov, 1968 (all diagnostic characters could be due to affine deformation and intra-specific variation)
- *sharovi* Gorochov, 2003, probable synonym of *primitivus* Sharov, 1968 (all diagnostic characters could be due to affine deformation and intra-specific variation)
- *zerichini* Gorochov, 2003, and *longispeculum* Gorochov, 2003, all probable synonyms of *libelluloides* Sharov, 1968 (all diagnostic characters could be due to affine deformation and intra-specific variation)
- *reductus* Gorochov, 2003, *venosus* Gorochov, 2003, *intermedius* Gorochov, 2003, *latispeculum* Gorochov, 2003, *bispeculum* Gorochov, 2003, and *modestus* Gorochov, 2003, all probable synonyms of *ovalis* Sharov, 1968 (all diagnostic characters could be due to affine deformation and intra-specific variation).

***Gigatitanidae* nom. Sharov, 1968, dis.-typ.n.:**

extensus Sharov, 1968

magnificus Sharov, 1968

vulgaris Sharov, 1968

Species of uncertain validity:

ovatus Sharov, 1968, *similis* Sharov, 1968: 201, *curtis* Sharov, 1968, all probable synonyms of *vulgaris* Sharov, 1968 (all diagnostic characters could be due to affine deformation and intra-specific variation).

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