

Groundplan, nomenclature, homology, phylogeny, and the question of the insect wing venation pattern

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ABSTRACT

The debate on the homologization of the wing venation of Orthoptera and some stem-Orthoptera is connected to the question of insect wing venation groundplan. This broader topic can be seen as the ‘serial paradigm’ vs. the ‘M5 paradigm’ debate. Unlike implied elsewhere, it is demonstrated that homology hypotheses developed under the two different paradigms have significantly different implications in terms of phylogeny, hence evolutive history at the level of Pterygota. Evidence in support of one paradigm or the other is critically reviewed. Wing veins that are arguably not homologous have been interpreted as M5 based on superficial similarity, and these interpretations do not withstand scrutiny. Based upon our current knowledge, the serial pattern is to be preferred.

KEY WORDS: serial pattern, M5 pattern, Pterygota.

INTRODUCTION

Modern attempts to establish homologies in wing venation across winged insects are based on two different paradigms. The serial pattern paradigm posits the occurrence of main veins dichotomizing into two sectors, the anterior one being convex (*i.e.* elevated), the posterior one being concave (*i.e.* located in a depression) (Lameere 1922, 1923). This pattern is followed by Kukalová-Peck (1991) and Béthoux & Nel (2002), among other contributions and authors. It is referred to as ‘classical’ by Béthoux (2007) and ‘metameric’ by Rasnitsyn (2007). On the other hand, the M5 pattern paradigm posits that the first fork of the Media gives rise to an anterior stem MA + MP and a posterior M5, the latter being convex. Additionally, the M5 pattern paradigm posits that the cubital system emits concave branches only [“Cubital vein (Cu) dichotomised subbasally into anterior CuA and posterior CuP, both concave (unless and until CuA merges with M5)”]; Rasnitsyn 2002a: 76]. The convexity of CuA as observed in most winged insects is supposedly due to the fusion of M5 with CuA [“[the] convex posteriormost branch of M, conventionally termed M5, the fusion of which with the primarily concave vein results in the familiar convex CuA”]; Rasnitsyn 2007: 342]. In summary, the serial pattern and the M5 pattern differ by the absence or presence of a posterior convex sector of M (M5), respectively, and the position of CuA at its origin, convex or concave, respectively.

A discussion initiated by Gorochov (2005) regarding the wing venation homologization developed by Béthoux & Nel (2001) and Béthoux & Nel (2002) for Orthoptera and Archaeorthoptera (including Orthoptera and some stem-Orthoptera), respectively, prompted two recent contributions. The former is my reply to Gorochov (2005) (Béthoux

2007), in which I mainly argue that the interpretation by Sharov (1968, 1971), followed by Gorochov (1995), is not consistent with the serial pattern, while that of Béthoux & Nel (2001, 2002) is. The second is a comment by Rasnitsyn (2007) on Béthoux’s vs. Sharov-Gorokhov’s wing venation debate, in which the author extends the debate to the wing venation pattern of winged insects as a whole, and relegates the problem on Orthoptera wing venation to a mere nomenclatural issue. This new debate is actually connected to the ‘serial wing venation pattern paradigm’ vs. the ‘M5 wing venation pattern paradigm’.

A reply to Rasnitsyn on the topic is necessary, as the author overlooked several aspects relevant for this discussion. There are several points to be addressed. First I argue that, under the M5 pattern paradigm, Rasnitsyn (2007) did not consider all possible interpretations of propositions by Sharov (1968) and Béthoux & Nel (2002). Implications of all interpretations onto phylogenetic hypotheses, under the serial pattern and the M5 pattern paradigms, will then be considered. I review evidence supporting the M5 pattern paradigm as listed by Rasnitsyn (2007), starting with a reconsideration of the claim that M5 occurs in Orthoptera and Plecoptera. I discuss the evidence in support of the serial pattern. Finally I apply parsimony at the level of the paradigms.

MATERIAL AND METHODS

Wing venation abbreviations are repeated herein for convenience: ScP, posterior Subcosta (sometimes referred to as Sc in the literature); R, Radius; RA, anterior Radius; RP, posterior Radius (sometimes referred to as Rs in the literature); M, Media; MA, anterior Media; MP, posterior

Media; Cu, Cubitus; CuA, anterior Cubitus; CuP, posterior Cubitus; AA, anterior Analis; AA1: first anterior anal. Where relevant, I use the nomenclature of CuP branches elaborated by Béthoux & Nel (2002) for Archaeorthoptera, itself based on that of Orthoptera (Béthoux & Nel 2001): CuPa, anterior branch of CuP; CuPa α , anterior branch of CuPa; CuPa β , posterior branch of CuPa; CuPb, posterior branch of CuP. The abbreviation 'M5' refers to a putative branch of M which is supposedly a convex posterior sector of the Media.

Specimens referred to as PIN are housed at the Palaeontological Institute of the Russian Academy of Science (Moscow, Russia). The specimen referred to as IWC OB (accounting for Insect Wing Collection Olivier Béthoux) belongs to my personal collection, temporarily housed in the Museum of Zoology, State Natural History Collections, Dresden (Germany).

Venation patterns and vein widths were drawn with a stereomicroscope and camera lucida directly from the fossil surface, both dry and under ethanol. The holotype of *Prophalangopsis obscura* (housed at the NHM, London) was positioned so that light produced by a light table passed through the wings (Fig. 2.1,2). An optic fiber was used for the Fig. 2.3. Hind wings of Mantodea illustrated on Fig. 6 were cut off and mounted on slides in Euparal medium. Photographs presented on Figs 2, 6.1,3 were taken with light produced from a light table, using a digital camera Canon EOS 400D and a 50mm Macro lens, coupled with an elongation tube as necessary. High magnification photographs (Fig. 6.2,4) were taken with a Zeiss AxioCam MRc 5 installed on a microscope Nikon Eclipse 600, driven by the software AxioVision 4.4. Original photographs were processed using Adobe Photoshop 7.0. Pieces of dust were erased manually on the photograph presented on Fig. 6.1 using the clone stamp tool. In case of suspicion of 'excessive cleaning', I offer to provide the original file on request. For convenience, Linnean taxonomy will be followed.

In the following I understand 'neoptery' as the capacity to fold wings back on the abdomen, I apply the adjective 'neopteran' to species assigned to the Neoptera, and 'neopterous' to insects exhibiting neoptery.

NOMENCLATURE AND HOMOLOGY

Rasnitsyn (2007: 342) states that, regarding Orthoptera and stem-Orthoptera wing venation, "because the MP of Sharov-Gorokhov entirely corresponds to my M5, I would like to state that Sharov's and my patterns are substantially identical and differ only nomenclatorially". It is true that Rasnitsyn's M5 can be used to point out the same structure as Sharov's MP Figs 1.1,2, respectively; see Rasnitsyn in Gorochov & Rasnitsyn (2002), and Sharov (1968), respectively]. However Rasnitsyn misses the point that the character states 'MP fused with CuA1', as interpreted by Sharov, and 'M5 fused with CuA', as hypothesized by Rasnitsyn, could co-occur if one interprets Sharov's MP and Rasnitsyn's M5 as M5 + MP in Orthoptera and stem-

Orthoptera (Fig. 1.3). In other words, under the M5 pattern, Sharov's MP is not necessarily homologous to Rasnitsyn's M5, *contra* Rasnitsyn (2007: 342).

This problem also affects Rasnitsyn's (2007) statement that Béthoux & Nel's (2002) CuA [elsewhere CuA + CuPa(α) in Rasnitsyn (2007); Fig. 1.4] is homologous to his M5. However CuA is not understood by Béthoux & Nel (2002) as homologous to Rasnitsyn's M5 but as homologous to CuA as in Storozhenko (2002), Kluge & Sinitshenkova (2002), Zherikhin (2002), and Rasnitsyn (2002d), among other researchers putatively 'inspired' by the M5 pattern [whose opinion about the M5 pattern is uncertain but that for the latter, provided that Rasnitsyn states that Gorochov & Rasnitsyn's (2002) nomenclature "reflects my opinion, not Gorokhov's" (2007: 342)]. An alternative interpretation demonstrates that the character states 'CuA (emerging from M + CuA) fused with CuP or its anterior branch' and 'M5 fused with CuA' can co-occur (Fig. 1.5). Therefore Béthoux & Nel's (2002) CuA and Rasnitsyn's (2007) M5 are not necessarily homologous.

It must be noticed here that Rasnitsyn's (2007) statement that "Béthoux's hypothesis, if realized consistently, requires a total renaming (in all insects) of M into M + CuA, and Cu into CuP" is not only trivial but also inaccurate. The nomenclature used by Storozhenko (2002) for Grylloblattida, Kluge & Sinitshenkova (2002) for Ephemeroptera, Zherikhin (2002) for Mantodea, and Rasnitsyn (2002d) for Embioptera, among other authors, need no modification for accommodating with the serial pattern, and Béthoux & Nel's (2002) hypothesis, which only regards Orthoptera and stem-Orthoptera. The situation is rather opposite: application of the M5 pattern would require a complete renaming of CuA as CuA + M5 in the above-mentioned contributions, as well as in a significant number of others.

HOMOLOGY AND PHYLOGENY

As demonstrated above, Rasnitsyn's (2007: 343) statement that "it should simply be accepted that the vein termed the median by Sharov is named the same by me and M + CuA by Béthoux. Respectively, Sharov's MP is myself M5 and Béthoux's CuA, while Cu of Sharov and myself is CuP of Béthoux" does not take into account all possible interpretations. This view of the problem overlooks the impact of a choice of one interpretation or the other onto phylogenetic hypotheses. At the level of Pterygota, the structure indicated by an arrow on Fig. 1 either is (1) MP (+M5) that fuses with CuA1 (Fig. 1.2,3), this character state constituting a putative apomorphy of Orthoptera (but see Sharov 1962), (2) CuA (+M5) that fuses with CuP (Fig. 1.4,5), this character state constituting a putative apomorphy of a taxon including Orthoptera and stem-Orthoptera, or (3) M5 that fuses with CuA (Fig. 1.1), which is considered as a plesiomorphy under the M5 paradigm, the character state being considered as apomorphic of (most?) winged insects according to Rasnitsyn's (2002a) diagnosis of Scarabaeona (= Pterygota). Hence the problem at hand

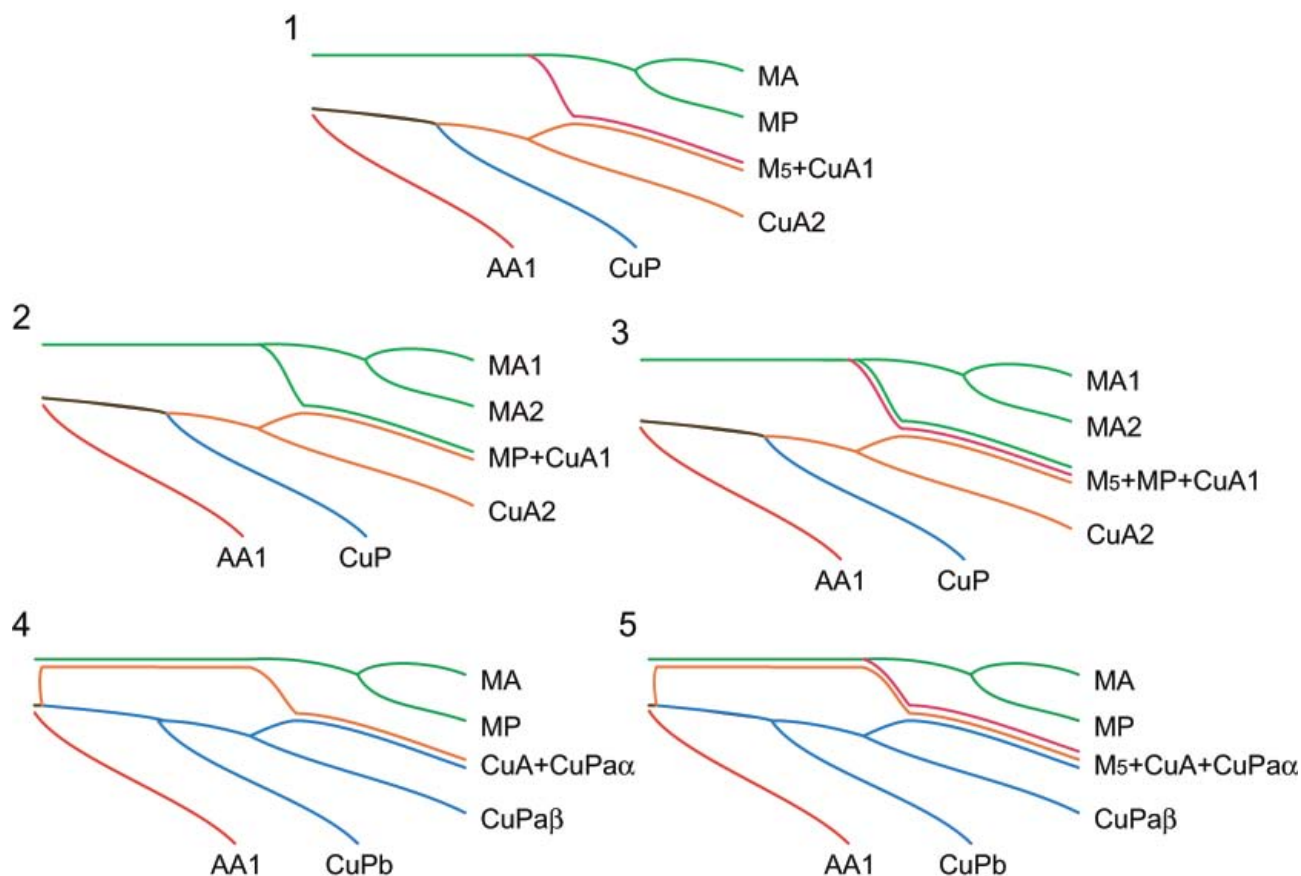


Figure 1. Possible interpretations of the medio-cubital area in Archaeorthoptera and Orthoptera (colour-coding as follows: green, median system but M5; pink, M5; brown, Cu; orange, CuA; blue, CuP; red, AA1; see text for abbreviations): 1 – Interpretation by Rasnitsyn in Gorokhov & Rasnitsyn (2002). 2 – Interpretation by Sharov (1968). 3 – Possible re-interpretation of Sharov's (1968) proposition under the M5 wing venation pattern paradigm. 4 – Interpretation by Béthoux & Nel (2001, 2002). 5 – Possible re-interpretation of Béthoux & Nel's (2001, 2002) proposition under the M5 wing venation pattern paradigm.

relates to the position of Orthoptera within winged insects, and the proper identification of stem-Orthoptera and stem-Pterygota.

Likewise the position of the branching of M into MA and MP, as well as the number of branches of the respective veins, is different under Sharov's interpretation (Fig. 1.2; see also Fig. 1.3) on one hand, and Rasnitsyn's and Béthoux & Nel's interpretations (Fig. 1.1, and Fig. 1.4,5, respectively) on the other. Similarly the location of the branching of Cu into CuA and CuP, the respective number and location of Cu vein sectors, are different under Sharov's and Rasnitsyn's interpretations on one hand (Fig. 1.1,2, respectively; see also Fig. 1.3), and Béthoux & Nel's interpretations on the other (Fig. 1.4; see also Fig. 1.5). The impact of these characters (states) at the level of Pterygota is unknown, but they definitely must be considered.

Therefore I argue that the polemic on Orthoptera wing venation pattern is not a mere nomenclatural problem, as implied by Rasnitsyn (2007), but is fundamental for phylogeny hypotheses at the level of Pterygota. At this step it is then essential to compare respective evidence in support of the M5 and serial pattern paradigms.

DISCUSSION ON EVIDENCE SUPPORTING THE M5 PATTERN

Regarding Orthoptera, the same vein has been interpreted as MP by Sharov (1968) and Gorokhov (1995), M5 by Rasnitsyn in Gorokhov & Rasnitsyn (2002), and CuA by Béthoux & Nel (2001). The vein the nature of which is under scrutiny is indicated by * on Fig. 2.1 and in the following. Interpretations by Sharov (1968) (see Fig. 1.2) and Rasnitsyn in Gorokhov & Rasnitsyn (2002) (see Fig. 1.1) predict the occurrence of a single trachea (as it is, the median trachea) in the stem that gives rise to the vein *. On the other hand, the interpretation of Béthoux & Nel (2001) (see Fig. 1.4) predicts that the stem from which diverges the vein * is provided with two tracheae, M and CuA. In order to determine the nature of the vein *, I investigated the wing morphology of the extant species *Prophalangopsis obscura*, which is widely recognized as a plesiotypic member of Ensifera (Zeuner 1939, Sharov 1968). I observed two tracheae in forewings of this species (Fig. 2). A narrow trachea (indicated as M on Fig. 2.2) gives rise to veins that are consistently interpreted as MA and MP by Rasnitsyn in Gorokhov & Rasnitsyn (2002) and Béthoux

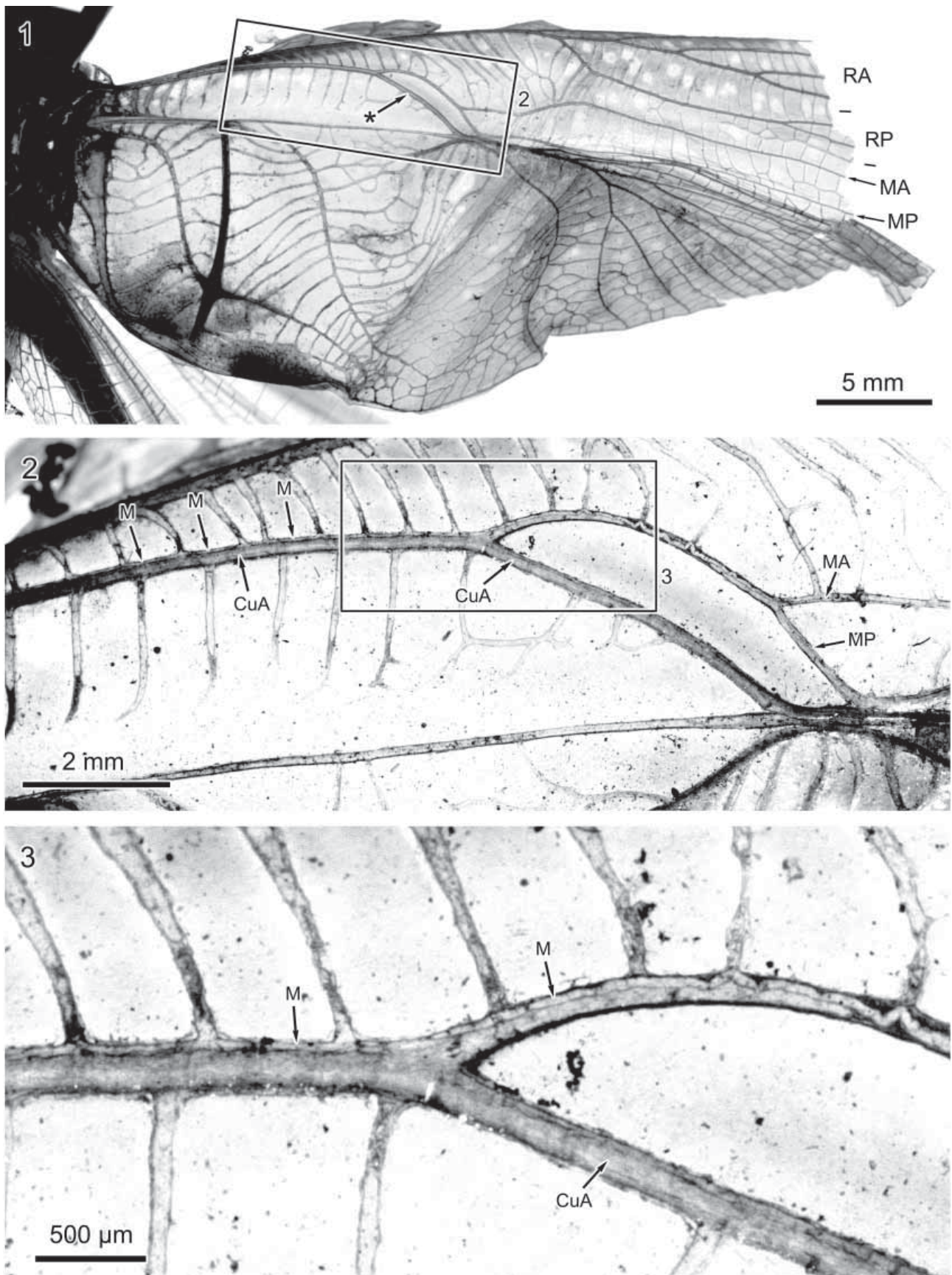


Figure 2. *Prophalangopsis obscura* (Orthoptera: Ensifera; holotype specimen, extent). 1 – Dorsal view of the right forewing [* indicates the structure interpreted as MP by Sharov (1968), M5 by Rasnitsyn in Gorokhov & Rasnitsyn (2002), and CuA by Béthoux & Nel (2001, 2002)]. 2 – Detail of the right forewing as indicated on 1. 3 – Detail of the right forewing as indicated on 2.

& Nel (2001). In other words, it likely is M. This narrow trachea is located anteriorly to a broader trachea running in the same tubular structure (indicated as CuA on Fig. 2.2). The median trachea does not fork at the level of the divergence of the vein * (Fig. 2.2,3). Therefore the median system does not take part in the composition of the vein *. This observation is consistent with the prediction that can be drawn from the interpretation by Béthoux & Nel (2001). No M5 could be evidenced in Orthoptera, and MP does not take part in the composition of vein *.

Béthoux (2005a) showed that the serial pattern is to be preferred by demonstrating that, in Plecoptera, CuA is convex from its origin, before any connection with another structure. Rasnitsyn (2007: 343) argued that “the change in the vein position is in my opinion not a very rare phenomenon [...] and, when a vein changes position along its length (as is the case of CuA becoming convex after its fusion with M5), the boundary between its convex and concave parts may shift easily”, a proposition that can be taken into account (pers. obs. in Palaeodictyopteroidea, Orthoptera, Titanoptera). However it is unfortunate that Rasnitsyn uses as an example the problem under scrutiny, hence providing a circular reasoning. Later on Rasnitsyn (2007) explicitly interpret Béthoux’s (2005a) arculus in stonefly wings as M5: “the vein termed the arculus by Béthoux (2005) looks like the typical M5 in the hind wings of most stoneflies figured by him; thus the same homology of arculus apply to the forewing as well” (my emphasis). However, it has never been proven that the arculus is provided with a trachea in hind wings of stoneflies, which would indicate its origin from a main vein. On the contrary, Béthoux (2005a) demonstrated that the arculus is free of trachea in forewings of stoneflies, hence is not a main vein. Here Béthoux’s (2005a) claim is independent of the vein position argument (convex or concave), which importance is minored by Rasnitsyn (2007; see above). Coupled with the absence of arculus in forewings of *Austroperla cyrene*, and the occurrence of two arculuses in forewings of several specimens of *Pteronarcys californica*, Béthoux (2005a) argued that the arculus in forewing of Plecoptera is a secondarily strengthened cross-vein. Hence there is no structure that can be identified as M5 in forewings of Plecoptera. Using Rasnitsyn’s deductive approach, this applies to hind wings as well.

Resulting from this argument, the vein sector CuA is convex from its origin in Plecoptera, which is an anomaly under the M5 paradigm (under which Cu is supposedly dichotomised into anterior concave CuA). One would then have to make the additional hypothesis that a fusion of M5 with CuA occurs at the wing base, but this is unproven and this proposition is not followed by Rasnitsyn (2007).

Rasnitsyn (2007) provides a number of references he considers as demonstrative of the occurrence of M5 in various taxa. I will discuss the presumed evidence following a taxonomic order. The reference to Sharov & Sinitshenkova (1977: fig. 2) concerns the fossil order Palaeodictyoptera. The authors indicate a sclerotized and oblique structure occurring between M and CuA on their restoration of

fragmentary remains of *Parathesoneura carpenteri*, they interpret as M5. Based on the photograph of the species holotype provided in Belayeva *et al.* (fig. 140), I observed that strong cross-veins occur between CuA (simple) and CuP (branched). This leaves open the possibility that the so-called M5 is such a strong cross-vein. This proposition is supported by the fact that no structure interpretable as M5 is described in the only known specimen of *Parathesoneura anfractuosa* (Sharov & Sinitshenkova 1977: fig. 2.d), a relative of *P. carpenteri* (if not synonym). In addition, Béthoux *et al.* (2007: fig. 1) illustrated a palaeodictyopteran wing exhibiting cross-veins of variable strength occurring in all areas between main veins. The organization exhibited by *Parathesoneura carpenteri* is not conclusive.

The reference to Vignon (1929: pl. II fig. 1) concerns the holotype of the palaeodictyopteran *Archaeomegaptilus kiefferi*. As interpreted by Vignon (1929), a marked structure ‘j’ is located between the veins ‘MA’ and ‘CuA₁’. Later to this connection, ‘CuA₁’ is stronger. Vignon’s ‘j’ is arguably a main vein which continues as a strong vein and reaches the posterior wing margin. Interpreting ‘j’ as M5 is consistent with the M5 paradigm. However, by its strength, ‘j’ is similar to the anterior sectors of R and M. And alike RA and MA, it is simple. These observations suggest that ‘j’ is the anterior sector of Cu. Vignon’s CuA would then be CuP, and CuA would be fused with M at the wing base. Therefore, a serial-pattern-based interpretation is plausible. This species is known from a single specimen and its phylogenetic position cannot be ascertained independently from the homologization of ‘j’ structure.

Rasnitsyn (2007) refers to Vignon (1929: pl. II fig. 2), presenting a photograph of a forewing of *Dictyoptilus sepultus* (Palaeodictyoptera), in which no structure is referred to as ‘j’ or ‘M5’. The sector CuA is concave at its origin, connects to M, and turns convex. Because CuA connects to M, there is no evidence of a free M5. In *Dictyoptilus peromapteroides*, CuA does not connect to M, and there is no strong structure located between CuA and M (Kukalová 1969: fig. 43). Therefore, the shift in the position of CuA cannot be explained by the fusion with a hypothetical M5.

Also regarding the Palaeodictyoptera, Rasnitsyn (2007) mentions Sinitshenkova (1979), without reference to a peculiar figure. In this contribution, the family Tchirkovaeidae is erected. In the diagnosis of the family Sinitshenkova (1979) mentions a “remainder of M5 connecting base of M to base of CuA”. It is arguable whether this ‘remainder’ is indicative of a main vein or of a strengthened cross-vein. It is unfortunate that parts interpreted as M5 are not indicated on the figures. As a result, interpretations of the author are difficult to follow. Notably, the differences between the wing venation of the specimens 3115/29 (fig. 4a; forewing) and 3115/157 (fig. 5a; hind wing), both considered as rudiments of nymphal wings of *Tchirkovaea guttata*, are not explained, and locating M5 in the former is not evident.

It is important to assert here that there is no structure that can be interpreted as M5 in the great majority of the Palaeodictyoptera (Carpenter 1992: figs 17.1,3,4,6-12,

18.1,3-4, 19, 20.2, 21.1,6,8, 22-27, 28.6; among other contributions, see also Carpenter 1967: plates 8,10, fig. 1,3; Kukulová 1969a: figs 1-11,13,17,19,20,22,24,26,28; Kukulová 1969b: figs 29-33,38-41,43,44,46,49; Kukulová-Peck 1971: figs 1,3-15; Brauckmann 1991: figs 1-4, 11-14; Brauckmann & Herd 2002: fig. 11; Béthoux *et al.* 2007: fig. 1). In several nymphs of Palaeodictyoptera, no structure interpretable as M5 can be pointed out (Carpenter & Richardson 1971; interpretation provided by Sharov & Sinitshenkova 1977: fig. c is not positively supported by photographic evidence). Rasnitsyn's (2007) position holds only if one considers that the few taxa exhibiting a putative M5 are stem representatives of the group, but there is no evidence independent of the occurrence of M5 supporting this view. In addition a loss of M5 must be advocated for taxa listed above.

Regarding the palaeodictyopteroidean orders Diaphanopteroidea and Megasecoptera, Rasnitsyn refers to the text-figs. 1-3 in Kukulová-Peck & Brauckmann (1990; 'st') as demonstrative of the occurrence of a M5, as it is in Diaphanopteroidea (he refers to this data also as in Rasnitsyn & Quicke 2002: text-fig. 150). However Kukulová-Peck & Brauckmann (1990) interpreted the corresponding structure as a secondarily strengthened cross-vein. A strikingly similar structure occurs between R/RP and MA in these taxa, and it has never been interpreted as a main vein. The similarity between these structures is also supported by the fact both CuA and MA are effectively concave (or neutral) at their origin and turn convex once connected to these structures. No convex posterior stem of RP has ever been advocated for explaining the shift of position of MA (see also Vignon 1929: pl. II, fig. 2, in which there is no cross-vein occurring between MA and RP, but MA is concave

at its origin), therefore I see no reason to advocate such a convex posterior stem for explaining the shift of CuA. I see no reason not to follow Kukulová-Peck & Brauckmann (1990), and consider that CuA, alike MA, is connected to the vein sector anterior to it by a strengthened cross-vein. Regarding the Megasecoptera, it is worth noticing that there is no structure interpretable as M5 in known nymphal wings (Carpenter & Richardson 1968).

The reference to Sinitshenkova (1979) concerns 'permothemistidan' insects, considered as members of the order Megasecoptera (Sinitshenkova 2002) or sister-group related to it (Grimaldi & Engel, 2005). Indeed CuA is concave (or neutral) before being connected to a sclerotized structure located between M and CuA. However, this structure can equally be interpreted as M5 or as a cross-vein. In any case, permothemistidan insects are not considered as stem-representatives of palaeodictyopteroidean insects (Sinitshenkova 2002, Grimaldi & Engel, 2005).

In summary, diaphanopteroidean, megasecopteran, and permothemistidan insects, as well as some palaeodictyopteran insects exhibit a CuA that is concave (or neutral) at its origin and turns convex at some point of its course, usually once connected to a structure located between M and CuA (but in *D. Peromapteroides*, and see below). This organization applies to MA as well, which is connected to R or RP *via* a cross-vein. It is then plausible to consider that CuA is connected to M *via* an homologous structure, *i.e.* a cross-vein. This proposition is supported by the organization exhibited by representatives of the family Eukulojidae, assigned by Sinitshenkova (2002) to the Dictyonaurida (=Palaeodictyoptera), in which wings are totally free of cross-veins. No M5 can be identified. Nonetheless, MA and CuA are concave (or neutral) at their origin and turn convex at some point (Fig. 3).

Rasnitsyn (2007) lists the figs 12-14 in Kukulová-Peck (1985), on which a strut located between M and CuA is indicated on wings of *Lithoneura* spp.. This taxon might be representative of Ephemeroptera. However Kukulová-Peck's (1985) observations and interpretations were challenged by Willmann (1999), who reports the absence of this 'strut'. At least this case is not conclusive.

Rasnitsyn (2007) refers to the fig. 87 in Belayeva *et al.* (2002) as indicative of the occurrence of M5, as it is in mayflies. However, no M5 is referred to in this figure, nor is in the diagnosis of Ephemeroptera in the corresponding contribution (Kluge & Sinitshenkova 2002). Rasnitsyn (2007) also mentions the figs. 10B, C in Carpenter (1979), which are photographs of wing-pads of the Lower Permian mayfly *Protereisma americanum*. A putative M5 is not indicated on these photographs and was I unable to locate it. The serial pattern is readily applicable to mayfly wing venation indeed (Séguy 1959, Carpenter 1979).

Rasnitsyn (2007) states that the "most primitive Carboniferous Grylloblattida" exhibit a M5. He refers to the fig. 106 in Storozhenko (1998), on which the forewing of *Dalduba faticana* (Daldubidae; see Storozhenko 1996) is illustrated (see Fig. 4; see also Storozhenko 2002: fig. 397). However, rather than being a support, the morphol-

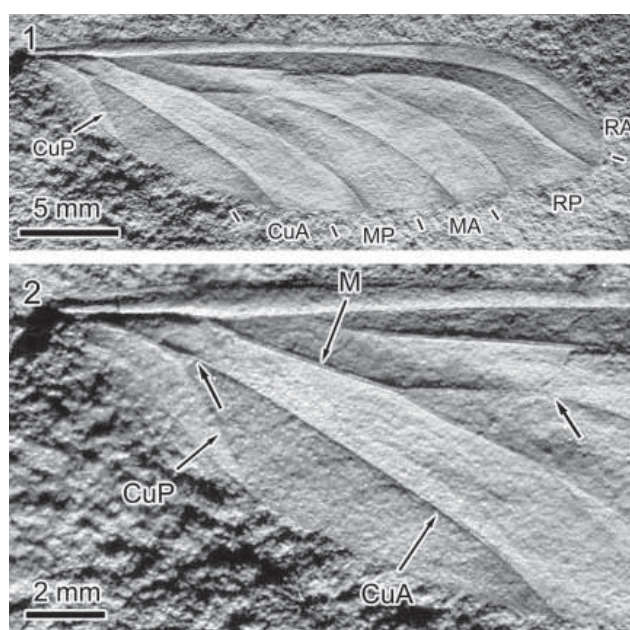


Figure 3. *Eukuloja cubitalis* (PIN 3353/6, right forewing, negative imprint, light-mirrored, flipped). 1. General view. 2. Detail of the wing base.

ogy exhibited by this species is an anomaly for the M5 paradigm. The structure interpreted as M5 by Storozhenko (1996), putatively followed by Rasnitsyn (2007), connects to a vein that is clearly convex from its point of divergence with CuP (the position of which is not debated), with no visible ‘shift’ of the vein position along its course (Fig. 4; evident concave veins are indicated by * of Fig. 4.2-3). Whichever interpretation is followed, this vein is CuA.

Therefore, CuA is convex from its origin, which contradicts the M5 paradigm axiom “Cubital vein (Cu) dichotomised sub-basally into anterior CuA and posterior CuP, both concave (unless and until CuA merges with M5)”. I tentatively interpreted Storozhenko’s (1996) M5 as a strengthened cross-vein similar to that occurring in Plecoptera. It must be noticed that the assignment of *D. faticana* to the Grylloblattida is not clearly grounded.

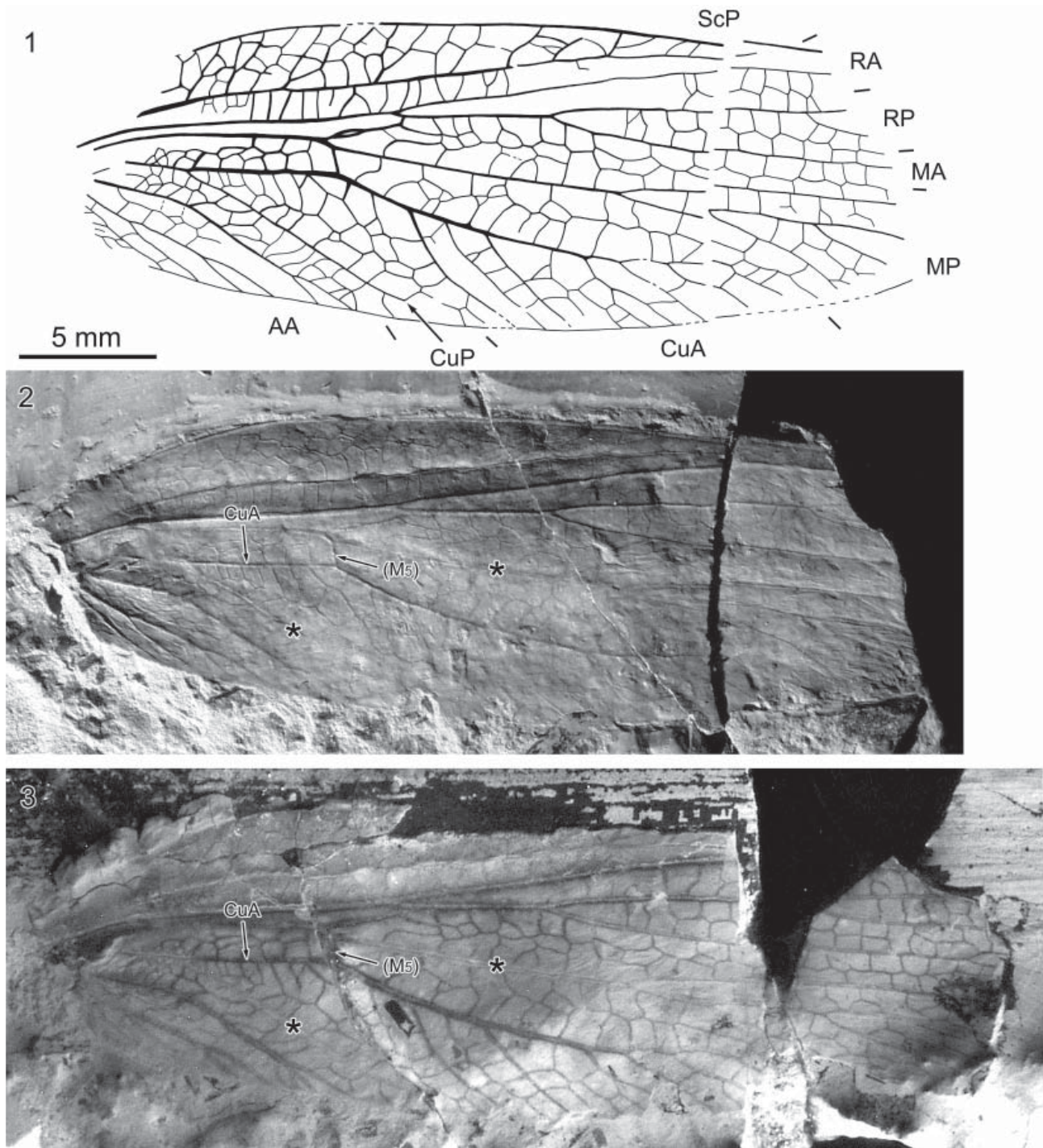


Figure 4. *Dalduba faticana* (holotype PIN 3115/77, right forewing). 1 – Drawing of the wing venation. 2 – Negative imprint (reversed; * indicate concave veins; ‘(M5)’ indicates the structure interpreted as M5 by Storozhenko 1996; a positive view of the specimen can be obtained by turning this figure upside down). 3 – Positive imprint (under ethanol; indications as in B).

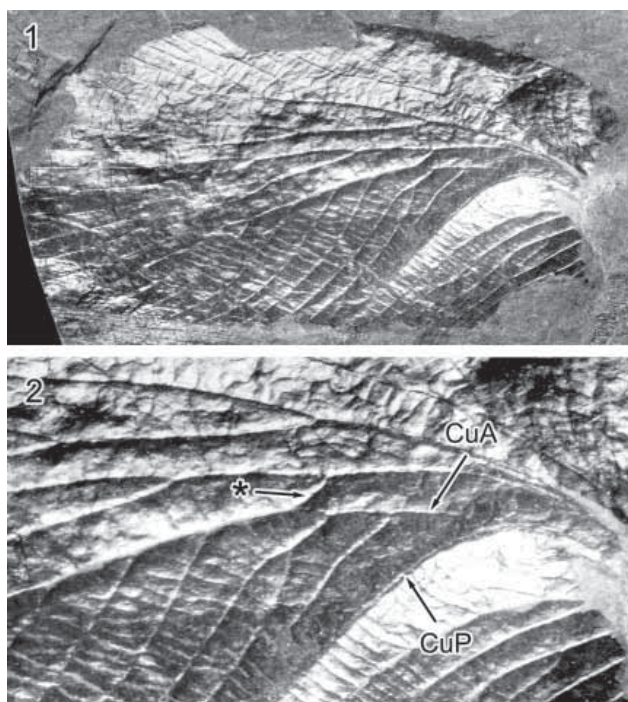


Figure 5. Undescribed stem-Dictyoptera or stem-Blattodea (reproduced from Laurentiaux 1958: pl. 31, fig. 5; Westphalian C, United-Kingdom). 1 – Right forewing, positive imprint. 2 – Detail of the right forewing as indicated on 1.

Rasnitsyn (2007) also refers to the fig. 109 in Storozhenko (1998), illustrating a hind wing assigned to *Vzeralduba nervosa* (Daldubidae; see Storozhenko 1996). A positive ordinal assignment of this taxon is impossible due to the fragmentary state of the available material. After the available information, it cannot be ruled out that *V. nervosa* is a genuine Archaeorthoptera, the so-called ‘M5’ being the vein sector CuA diverging from M + CuA.

In his diagnosis of the order Grylloblattida, Storozhenko (2002) states that “M5 [is] rarely present”. Following the phylogenetic scheme of this author, having M5 absent is considered as a character state synapomorphic of the node 2, encompassing the paraphyletic taxon Lemmatophorina, which is sister-group related to the rest of the Grylloblattida. The state exhibited by the sister-group (node 7, encompassing Protoperlina and Grylloblattina) is not specified but, considering that the presence of M5 is coded as apomorphic of the nodes 33, 54, 61, and 68, all nested deeply within the Protoperlina and Grylloblattina, one is likely to consider that neither Protoperlina nor Grylloblattina have a M5 but few inner taxa. In other words, the great majority of Grylloblattida do not exhibit any structure interpretable as M5, and have a CuA convex from its base. Moreover, the nature of the so-called M5 occurring in few ‘derived’ Grylloblattida is ambiguous: it can equally be interpreted as a secondarily strengthened cross-vein acquired at nodes 33, 54, 61, and 68 (see Béthoux *et al.* 2005, among others). Therefore there is no positive evidence that plesiotypic (or ‘primitive’) Grylloblattida exhibit a M5.

The contribution by Laurentiaux-Vieira & Laurentiaux (1980) is listed by Rasnitsyn (2007) as indicative of the occurrence of M5 in some Carboniferous ‘blattideans’ that are probable stem-Blattodea or stem-Dictyoptera. The authors indicate the occurrence of a sclerotized oblique structure located between M and CuA. They interpret this structure as an ‘anastomosing vein’. They provide no discussion about its origin. With respect to the M5 paradigm, however, the morphology exhibited by these taxa is an anomaly: again, the vein that is CuA (whichever interpretation is followed) is convex from its origin, without any shift of its position proximal and distal to the connection to the so-called M5. This absence of alteration of the position of CuA is conspicuous on specimens in which this structure is located distal to the first branches of CuA, which are also distinctly convex (Fig. 5). A number of undescribed taxa illustrated in Laurentiaux (1958) exhibit this organization.

Rasnitsyn (2007) lists the fig. 420 in Belayeva *et al.* (2002) as indicative of the occurrence of M5, as it is in the protelytropteran *Apachelytron transversum*. However, no M5 is indicated on this figure, nor is on any figure of the original description of the forewings of this species (Carpenter & Kukulová-Peck 1964; see also Kukulová-Peck 1991: fig. 6.20A). Haas & Kukulová-Peck (2001) provided a restoration of the same species with an oblique structure occurring between the so-called ‘MP’ and CuA, slightly stronger than surrounding cross-veins. However, no direct evidence was provided. Therefore, the proposition that M5 occurs in Protelytroptera is not positively grounded.

Rasnitsyn (2007) refers to illustrations of taxa I assigned to the Archaeorthoptera. The fig. 353 in Rasnitsyn (2002c) illustrates the holotype of *Eoblatta robusta*. The fig. 355 in Rasnitsyn (2002c) is based on the specimen NHM I.7279, assigned to *Ctenoptilus elongatus* by Béthoux & Nel (2004), and is considered as a close relative of *E. robusta* by Rasnitsyn (2002c) and Béthoux (2005c). First of all, no M5 is clearly indicated on the figures listed by Rasnitsyn (2007). Based on the same material and additional specimens, Béthoux & Nel (2004: fig. 7 and figs 9-11, respectively) described a convex stem (CuA/M5) diverging from M and fusing with a concave vein (CuPa/CuA) in these species, such as in *P. obscura* and other Orthoptera. This observation was corroborated by recent accounts on taxa that are putative relatives of *E. robusta* and *C. elongatus*, for which well-preserved specimens are known (Béthoux 2005c: figs 1, 2; Prokop & Ren 2007: figs 4,5,7). The vein referred to as CuA in these contributions could be interpreted as Rasnitsyn’s M5 or as M5 + CuA (see above), assuming that these fossil taxa are not related to Orthoptera. If so, unlike in the case of Grylloblattida, the presumed M5 connects to a concave vein. Because the course of tracheae cannot be investigated in these taxa, they provide support neither for the serial nor for the M5 pattern, as it conforms to both (but see below).

Likewise the fig. 356 in Rasnitsyn (2002c) illustrates a forewing of *Narkemina angustata* which venation conforms to the archaeorthopteran interpretation (Béthoux

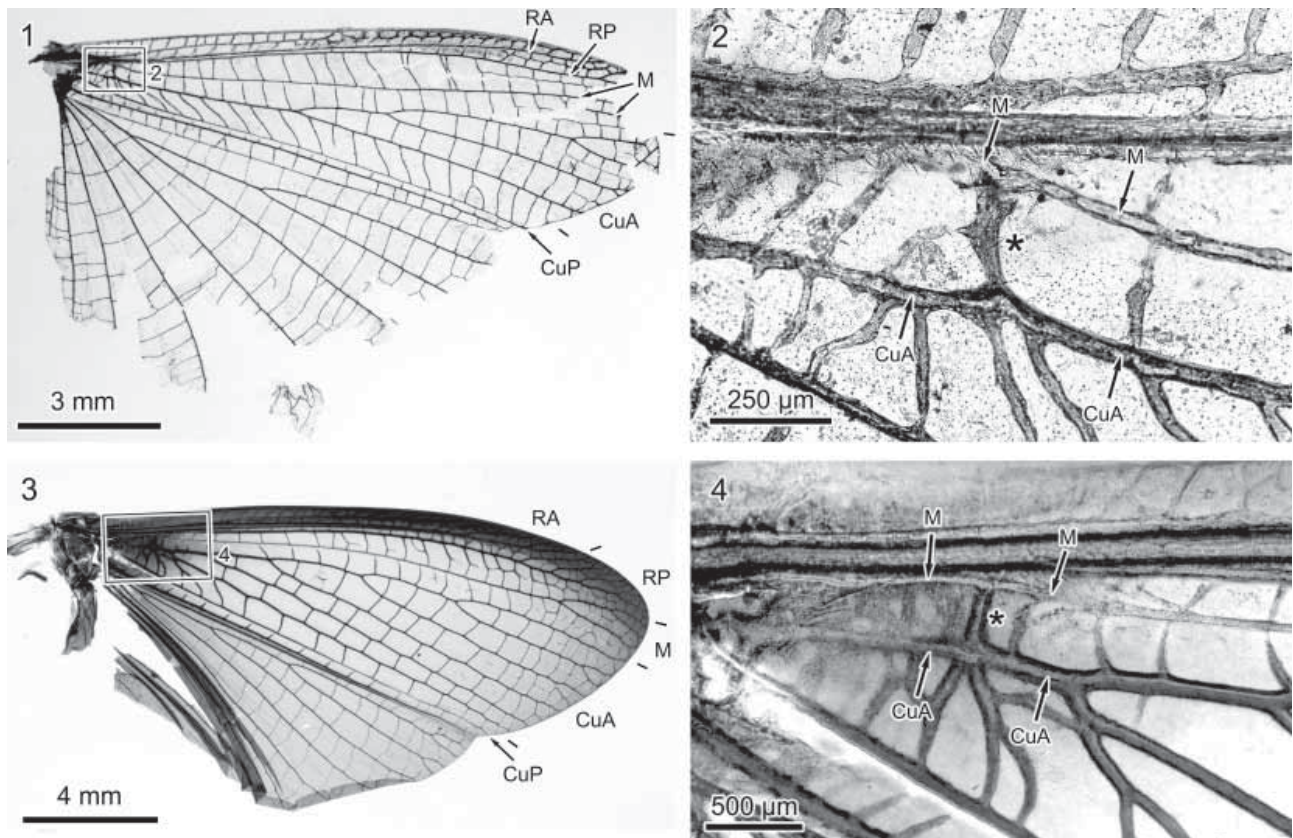


Figure 6. Hind wings of plesiotypic extent Mantodea. 1 – *Chaeteessa* sp., right hind wing, dorsal view (Dresden Museum of Zoology, Dresden, Germany). 2 – *Chaeteessa* sp., detail of the right hind wing as indicated on 1 (* is located on the right side of the arculus between M and CuA). 3 – *Metallyticus splendidus*, right hind wing, dorsal view (IWC OB 192). 4 – *Metallyticus splendidus*, detail of the right hind wing as indicated on 3 (* is located on the right side of the arculus between M and CuA).

2005b). The fig. 359 in Rasnitsyn (2002c) illustrates the holotype of *Protophasma dumasii*. No M5 is indicated on this figure and I presume that Rasnitsyn interprets as M5 the vein I (2003) interpreted as CuA. Drawings provided on the fig. 360 in Rasnitsyn (2002c), illustrating material belonging to the genus *Gerarus*, are based on literature data and are inaccurate. Béthoux & Nel (2003) revised the available material of *Gerarus* from Commeny (France) and found the wing venation of *Gerarus* to conform to the archaeorthopteran interpretation (Béthoux 2005b). Besides the fact that photographic evidence is lacking, the fig. 361 in Rasnitsyn (2002c) does not convincingly illustrate a contact of the so-called ‘M5’ with ‘CuA’. Once again, an archaeorthopteran interpretation, *i.e.* conforming to the serial pattern, is possible. Finally, despite its fragmentary state, the specimen illustrated by Bolton (1921: pl. 1, fig. 1) and listed by Rasnitsyn (2007) exhibit a venation consistent with an archaeorthopteran interpretation.

From this critical reappraisal, evidence listed by Rasnitsyn (2007) in support of the M5 wing venation pattern paradigm is not conclusive. Some rather constitute anomalies for this paradigm. Alternative interpretations consistent with the serial pattern can be provided without advocating complex hypotheses. It is worth mentioning that there

is no evidence of the occurrence of M5 in stem-Odonata (Riek & Kukulová-Peck 1984, Rasnitsyn 2002b). As indicated by various authors (Ragge 1955, Smart 1956, Sharov 1962, Balderson 1991, Zherikhin 2002, Deitz *et al.* 2003 ; among others), no M5 takes part in the wing venation of Mantodea. In mantodean hind wings the strongly sclerotized structure occurring between M and CuA is free of trachea (Fig. 6), hence cannot be considered as a main vein (*i.e.* cannot be M5), and no M5 occurs in nymphal wings. The same applies to the arculus in hind wings of Blattodea (pers. obs.; Ragge, 1955)

In summary, there is no positive evidence of the presence of a M5 in winged insects. The M5 paradigm is tenable in the case of Carboniferous non-panorthopteran archaeorthopteran, assuming that they are not directly related to Orthoptera (which definitely lack a M5, see above). Another aspect of Rasnitsyn’s (2007) argument is the occurrence of M5 in “earlier” or “most primitive” taxa. However, in all cases, this evidence is based on a mere circular reasoning, as the position of these taxa is based on the presumed occurrence of M5 only. When somehow tested by congruence with other characters, the occurrence of structure interpreted as M5 is found highly homoplastic, and not conclusively plesiomorphic (Storozhenko 2002).

DISCUSSION ON EVIDENCE SUPPORTING THE SERIAL PATTERN

Rasnitsyn (2007: 342) mentions that “Kukalová-Peck’s hypothesis suffers from a groundless conviction that the venation in the ancestor of winged insects was completely regular (metameric)”. In the meantime Béthoux *et al.* (2007) pointed out a regular serial organization of wing main veins occurring in several families of palaeodictyopteridan insects. In these taxa, anterior sectors of R, M, and Cu are all simple, while posterior sectors are all branched. This support for a serial homology is not based on veins position (convex or concave), but rather on the branching pattern itself. Coupled with the vein position evidence (anterior sectors are convex, posterior sectors are concave), support for the occurrence of a serially arranged venation pattern in palaeodictyopteridan insects is compelling. Since there is no consensus on the phylogenetic position of palaeodictyopteridan insects with respect to ‘palaeopteran’ taxa and Neoptera (compare Kukalová-Peck 1991, Rasnitsyn & Quicke 2002, and Grimaldi & Engel 2005), the relevance of this pattern to the whole winged insects is uncertain (Béthoux *et al.* 2007), though far from “groundless”.

The serial pattern suffers from no anomaly when applied to the wing venation of Ephemeroptera and Odonata (and respective stem-groups). The only anomaly concerns the Neoptera, in which a strongly convex MA is absent (Carpenter 1992). It must be noticed, however, that the median system has probably been the most modified system in neopteran insects. Its position in Mantodea and Phasmatodea, for example, is uncertain (in prep.). The first posterior branch of the Media is reduced or lost in the order Cnemidolestodea (Béthoux & Nel 2004, Béthoux 2005b, Béthoux & Nel 2005). More or less complete fusions of the anterior branch of M with RP are known in Orthoptera (Sharov 1968, 1971). Therefore, in Neoptera, the complete disappearance of MA, a loss of its convexity, or its complete fusion with the radial system, are all plausible hypotheses, although no positive evidence has ever been provided.

PARSIMONY APPLIED TO PARADIGMS

As mentioned above, the wing venation of several taxa assigned to the Archaeoptera by Béthoux & Nel (2002; and subsequent publications) equally fits in the serial and M5 pattern paradigms. For all other major pterygotan groups, the loss of the M5 (or a hypothetical fusion with CuA) must be advocated. A number of archaeopteranans can be excluded from the more derived taxon Panorthoptera as outlined by Béthoux & Nel (2002) [there is no objective reason for synonymising Panorthoptera *sensu* Béthoux & Nel (2002) with Polyneoptera as in Martins-Neto *et al.* (2007), as Dictyoptera, Embioptera, and Plecoptera, among other taxa commonly considered as of ‘polyneopteran affinities’, have never been considered as members of the Panorthoptera by Béthoux & Nel (2002)]. The remain-

ing taxa will be referred to as ‘stem-archaeopteran’ in the following. They are the eoblattid insects or Rasnitsyn (2002c).

Under the M5 paradigm and the Scarabaeones – Gryllones phylogenetic frame, ‘stem-archaeopteranans’ exhibit the putative plesiomorphic organization of the medio-cubital area at the level of Pterygota. There is no known phylogeny based on cladistic analysis including fossil and modern Pterygota. Thus I rely on phylogenetic analyses based on molecular data. They consistently found a monophyletic Neoptera (Wheeler *et al.* 2001a, 2001b, Hovmöller *et al.* 2002, Kjer 2004, Kjer *et al.* 2006, Mallatt & Giribet 2006), which contradicts the Scarabaeones – Gryllones hypothesis (Belayeva *et al.*, 2002). Placing stem-archaeopteran as sister-group of all other Pterygota would imply the gain of a convex MA, and the loss of neoptery and of an expanded hind wing anal fan in ‘paleopteran’ orders (‘stem-archaeopteranans’ lack a convex MA, are neopterous, and have an expanded hind wing anal fan; Rasnitsyn 2002c, Béthoux 2003, Béthoux & Nel 2004, Béthoux 2005b, 2005c, Béthoux & Nel 2005, Béthoux 2006, Prokop & Ren 2007). Under this ‘alignment’, assuming a monophyletic Palaeoptera, three steps are required (and up to six under various ‘paraphyletic Palaeoptera’ hypotheses). Under the serial pattern, following the venation interpretation by Béthoux & Nel (2002) and an assignment of stem-archaeopteran within Archaeoptera, *i.e.* within ‘polyneopteran’ orders, only a loss of MA (or of its convexity) must be advocated for Neoptera. This option requires a single step and should then be preferred.

CONCLUSION

Rather than being a mere nomenclatural problem, Rasnitsyn’s, Sharov’s, and Béthoux & Nel’s homology hypotheses of Orthoptera wing venation, either under the serial or the M5 pattern paradigms, have significantly different implications in terms of phylogeny at the level of Pterygota. Rasnitsyn’s (2007) mediation does not properly address Béthoux’s (2007) position regarding Sharov’s homology hypothesis (*i.e.* Sharov’s MP is CuA), but only Béthoux’s (2007) position regarding Rasnitsyn’s homology hypothesis as in Gorochov & Rasnitsyn (2002) (*i.e.* Rasnitsyn’s M5 is CuA). This point is addressed herein. New observations and literature data definitely suggest that Béthoux’s (2007) argument prevails over Gorochov’s (2005), the latter favouring Sharov’s homology hypothesis.

Structures that are arguably not homologous have been interpreted as M5 based on superficial similarity. The trachea filling the so-called M5 in Orthoptera does not belong to the median system but to CuA. The absence of trachea allowed the interpretation of the strengthened cross-veins occurring between M and CuA as M5 in Plecoptera to be discarded. No M5 can be identified in Ephemeroptera, Odonata, and Mantodea, among others. Numerous anomalies are not dealt with by the M5 pattern paradigm (as in

fossil Grylloblattodea, Blattodea). On the other hand, the serial pattern is supported by evidence based on the relative position of veins (convex or concave), and by the occurrence, in some taxa, of identical main vein branching patterns that are serially arranged.

Ultimately, following the M5 paradigm and placing non-panorthopteran archaeorthopterans as stem-pterygotans is not as parsimonious as following the serial pattern and placing these taxa in Neoptera. The serial pattern paradigm should be preferred unless CuA is considered as M5 + CuA in all winged insects. But this proposition is discarded by the conservative presumption favoured by Rasnitsyn (2007): under the serial pattern paradigm, it is unnecessary to advocate the presence of a M5 for establishing wing venation homologies among winged insects.

At this step it is worth quoting Rasnitsyn (2007: 343): “Béthoux also does not attach significance to the fact that the CuA in *common usage* is usually a richly branching vein, while CuP is in most cases simple or has few branches, whereas, in the pattern proposed by him, conversely, only CuP is multibranching” (my emphasis). Here maybe relies the evidence of an important methodological difference: Rasnitsyn elaborates homology, character state polarization, and phylogeny hypotheses in a single process. I attempt to make a distinction between these sets of hypotheses because it allows more or less independent tests of them. Under my opinion the performance of the latter approach is higher.

Lastly, Rasnitsyn (2007: 343) considers that “debate in general is not the most worthwhile occupation for thinking men”. On the opposite I consider that it is an essential occupation without which we would still believe that the Sun revolves around the Earth.

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REFERENCES

- BALDERSON, J. 1991. Mantodea. In: *The Insects of Australia, a textbook for students and researchers* (2nd ed.), NAUMANN, I. D. (Ed.), Melbourne University Press, Melbourne, Australia: 348-356.
- BELAYEVA, N. V., BLAGODEROV, V. A., DMITRIEV, V. Y., ESKOV, K. Y., GOROCHOV, A. V., IVANOV, V. D., KLUGE, N. Y., KOZLOV, M. V., LUKASHEVICH, E. D., MOSTOVSKI, M. B., NOVOKSHONOV, V. G., PONOMARENKO, A. G., POPOV, Y. A., PRITYKINA, L. N., RASNITSYN, A. P., SHCHERBAKOV, D. E., SINITSHENKOVA, N. D., STOROZHENKO, S. Y., SUKATSHEVA, I. D., VISHNIAKOVA, V. N., VRŠANSKÝ, P. & ZHERIKHIN, V. V. 2002. *History of Insects*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 517 pp.
- BÉTHOUX, O. 2003. *Protophasma dumasii* Brongniart, 1879, a link between Orthoptera and the ‘dictyopterid’ orders? *Journal of Orthoptera Research*, 12: 57-62.
- BÉTHOUX, O. 2005a. Wing venation pattern of Plecoptera (Neoptera). *Illiesia*, 1: 52-81.
- BÉTHOUX, O. 2005b. Cnemidolestodea (Insecta): an ancient order reinstated. *Journal of Systematic Palaeontology*, 3: 403-408.
- BÉTHOUX, O. 2005c. Reassigned and new basal Archaeorthoptera from the Upper Carboniferous of Mazon Creek (IL, USA). *Journal of Orthoptera Research*, 14: 121-126.
- BÉTHOUX, O. 2006. Revision of *Cacurgus* Handlirsch, 1911, a basal Pennsylvanian Archaeorthoptera (Insecta: Neoptera). *Bulletin of the Peabody Museum of Natural History*, 47: 29-35.
- BÉTHOUX, O. 2007. Archaeorthoptera wing venation nomenclature: a reply to Gorokhov. *Paleontological Journal*, 2007: 102-104.
- BÉTHOUX, O. & NEL, A. 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research*, 10: 195-198.
- BÉTHOUX, O. & NEL, A. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa*, 96: 1-88.
- BÉTHOUX, O. & NEL, A. 2003. Wing venation morphology and variability of *Gerarus fischeri* (Brongniart, 1885) sensu Burnham (Panorthoptera; Upper Carboniferous, Combray, France), with inferences on flight performances. *Organisms, Diversity & Evolution*, 3: 173-183.
- BÉTHOUX, O. & NEL, A. 2004. Some Palaeozoic ‘Protorthoptera’ are ‘ancestral’ orthopteroids: major wing braces as clues to a new split among the ‘Protorthoptera’. *Journal of Systematic Palaeontology*, 2: 285-309.
- BÉTHOUX, O. & NEL, A. 2005. Some Palaeozoic ‘Protorthoptera’ are ‘ancestral’ orthopteroids: major wing braces as clues to a new split among the ‘Protorthop-

- tera': corrigendum. *Journal of Systematic Palaeontology*, 3: 223.
- BÉTHOUX, O., NEL, A., LAPEYRIE, J. & GAND, G. 2005. New data on Paleozoic 'Grylloblattid' insects (Neoptera). *Journal of Paleontology*, 79: 125-138, 629-630.
- BÉTHOUX, O., NEL, A., SCHNEIDER, J. W. & GAND, G. 2007. *Lodetiella magnifica* nov. gen. and nov. sp. (Insecta: Palaeodictyoptera; Permian), an extreme case in wing morphology of palaeopterous insects. *Geobios*, 40: 181-189.
- BOLTON, H. 1921. A monograph of the fossil Insects of the British Coal Measures. Part I. Palaeontographical Society, 73: 1-80.
- BRAUCKMANN, C. 1991. Morphologie und Variabilität von *Homoioptera vorhallensis* (Insecta: Palaeodictyoptera; Ober-Karbon). *Geologia et Palaeontologica*, 25: 193-213.
- BRAUCKMANN, C. & HERD, K. J. 2002. Insekten-Fune aus dem Westfalium D (Ober-Karbon) des Piesberges bei Osnabrück (Deutschland). Teil 1: Palaeoptera. *Osnabrücker naturwissenschaftliche Mitteilungen*, 28: 27-69.
- CARPENTER, F. M. 1967. Studies on North American Carboniferous Insects. 5. Palaeodictyoptera and Megasecoptera from Illinois and Tennessee, with a discussion of the Order Sypharopteroidea. *Psyche*, 74: 58-84.
- CARPENTER, F. M. 1979. Lower Permian insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. *Psyche*, 86: 261-290.
- CARPENTER, F. M. 1992. Superclass Hexapoda. In: *Treatise on Invertebrate Paleontology*, KAESLER, R. L. (Ed.), The Geological Society of America and the University of Kansas, Boulder, USA.
- CARPENTER, F. M. & KUKALOVÁ-PECK, J. 1964. The structure of the Protelytroptera, with description of a new genus from Permian strata of Moravia. *Psyche*, 71: 183-197.
- CARPENTER, F. M. & RICHARDSON, E. S. 1968. Megasecopterous nymphs in Pennsylvanian concretions from Illinois. *Psyche*, 75: 295-309.
- CARPENTER, F. M. & RICHARDSON, E. S. 1971. Additional Insects in Pennsylvanian concretions from Illinois. *Psyche*, 78: 267-295.
- DEITZ, L. L., NALEPA, C. A. & KLASS, K.-D. 2003. Phylogeny of the Dictyoptera re-examined (Insecta). *Entomologische Abhandlungen*, 61: 69-91.
- GOROKHOV, A. V. 1995. System and evolution of the suborder Ensifera (Orthoptera). Part I. Proceedings of the Zoological Institute, Russian Academy of Sciences, 260: 1-224.
- GOROCHOV, A. V. 2005. Review of Triassic Orthoptera with descriptions of new and little known taxa. Part 1. *Paleontological Journal*, 39: 178-186.
- GOROKHOV, A. V. & RASNITSYN, A. P. 2002. 2.2.2.3. Superorder Gryllidea Laicharting, 1781 (=Orthopteroidea Handlirsch, 1903). In: *History of Insects*, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 293-303.
- GRIMALDI, D. & ENGEL, M. S. 2005. *Evolution of the Insects*. Cambridge University Press, New York, USA, 755 pp.
- HAAS, F. & KUKALOVÁ-PECK, J. 2001. Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). *European Journal of Entomology*, 98: 445-509.
- HOVMÖLLER, R., PAPE, T. & KÄLLERSJO, M. 2002. The Palaeoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. *Cladistics*, 18: 313-323.
- KJER, K. M. 2004. Aligned 18S and insect phylogeny. *Systematic Biology*, 53: 506-514.
- KJER, K. M., CARLE, F. L., LITMAN, J. & WARE, J. 2006. A molecular phylogeny of Insecta. *Arthropod Systematics & Phylogeny*, 64: 35-44.
- KLUGE, N. Y. & SINITSHENKOVA, N. D. 2002. 2.2.1.1.1.3. Order Ephemera Latreille, 1810. The true mayflies (= Ephemeroptera Hyatt et Arms, 1891 (s. l.); = Euephemeroptera Kluge 2000). In: *History of Insects*, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 89-97.
- KUKALOVÁ, J. 1969a. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commeny, France. Part 1. *Psyche*, 76: 163-215.
- KUKALOVÁ, J. 1969b. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commeny, France. Part 2. *Psyche*, 76: 439-486.
- KUKALOVÁ-PECK, J. 1971. The structure of *Dunbaria* (Palaeodictyoptera). *Psyche*, 78: 306-318.
- KUKALOVÁ-PECK, J. 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). *Canadian Journal of Zoology*, 63: 933-955.
- KUKALOVÁ-PECK, J. 1991. Fossil History and the Evolution of Hexapod Structures. In: *The Insects of Australia, a textbook for students and researchers* (2nd ed.), NAUMANN, I. D. (Ed.), Melbourne University Press, Melbourne, Australia: 141-179.
- KUKALOVÁ-PECK, J. & BRAUCKMANN, C. 1990. Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany. *Canadian Journal of Zoology*, 68: 1104-1111.

- LAMEERE, A. 1922. Sur la nervation alaire des Insectes. Bulletin de la Classe des Sciences de l'Académie Royale de Belgique, Bruxelles: 138-149.
- LAMEERE, A. 1923. On the wing-venation of insects. Psyche, 30: 123-132.
- LAURENTIAUX-VIEIRA, F. & LAURENTIAUX, D. 1980. Nouvelle contribution à la connaissance du genre Westphalien *Manoblatta* Pruvost (Blattaires, Archymylacridiens). Annales de la Société Géologique du Nord, 99: 415-423.
- LAURENTIAUX, D. 1958. Contribution à l'étude des insectes carbonifères. Université de Paris, 1958.
- MALLATT, J. & GIRIBET, G. 2006. Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. Molecular Phylogenetics and Evolution, 40: 772-794.
- MARTINS-NETO, R. G., GALLEGO, O. F., BRAUCKMANN, C. & CRUZ, J. L. 2007. A review of the South American Palaeozoic entomofauna Part I: the Ischnoneuroidea and Cacurgoidea, with description of new taxa. African Invertebrates, 48: 87-101.
- PROKOP, J. & REN, D. 2007. New significant fossil insects from the Upper Carboniferous of Ningxia in northern China (Insecta: Palaeodictyoptera, Archaeorthoptera). European Journal of Entomology, 104: 267-275.
- RAGGE, D. R. 1955. The wing-venation of the Orthoptera Saltatoria with notes on dictyopteran wing-venation. British Museum (Natural History), London, United Kingdom, vi + 160 pp.
- RASNITSYN, A. P. 2002a. 2.2. Subclass Scarabaeona Laicharting, 1781. The winged insects (=Pterygota Lang, 1888). In: History of Insects, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 75-83.
- RASNITSYN, A. P. 2002b. 2.2.1.1.2 Superorder Libellulidea Laicharting, 1781 Order Odonata Fabricius, 1792. The dragonflies. In: History of Insects, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 97-105.
- RASNITSYN, A. P. 2002c. 2.2.2. Infraclass Gryllones Laicharting, 1781. The grylloneans (=Polyneoptera Martynov, 1938). In: History of Insects, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 254-262.
- RASNITSYN, A. P. 2002d. 2.2.2.2.4. Order Embiida Burmeister, 1835. The web-spinners (=Embioptera Shipley, 1904). In: History of Insects, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 291-293.
- RASNITSYN, A. P. 2007. On the discussion of the wing venation of (Archae)Orthoptera (Insecta). Paleontological Journal, 41: 341-344.
- RIEK, E. F. & KUKALOVÁ-PECK, J. 1984. A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta, Odonatoidea) and basic character states in pterygota wings. Canadian Journal of Zoology, 62: 1150-1166.
- SÉGUY, E. 1959. Introduction à l'étude morphologique de l'aile des insectes. Mémoires du Muséum National d'Histoire Naturelle, Paris, Nouvelle série, (A), 21: 1-248.
- SHAROV, A. G. 1962. Redescription of *Lithophotina floccosa* Cock. (mantodea) with some notes on the mantodean wing venation. Psyche, 69: 102-106.
- SHAROV, A. G. 1968. Filogeniya orthopteroidnykh nasekomykh. Trudy Paleontologicheskogo instituta, Akademiya Nauk SSSR, 118: 1-216.
- SHAROV, A. G. 1971. Phylogeny of the Orthopteroidea. Israel Program for Scientific Translations, Jerusalem, Israel, vi + 251 pp.
- SHAROV, A. G. & SINITSHENKOVA, N. D. 1977. New Palaeodictyoptera from the USSR. Paleontological Journal, 11: 48-63.
- SINITSHENKOVA, N. D. 1979. A new family of the Palaeodictyoptera from the Carboniferous of Siberia. Paleontological Journal, 13: 192-205.
- SINITSHENKOVA, N. D. 1980. A revision of the order Permothemistida (Insecta). Paleontological Journal, 14: 97-112.
- SINITSHENKOVA, N. D. 2002. 2.2.1.2.3. Superorder Dictyoneuridea Handlirsch, 1906 (=Palaeodictyopteroidea). In: History of Insects, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 115-124.
- SMART, J. 1956. On the wing venation of *Chaeteessa* and other mantids (Insecta: Mantodea). Proceedings of the Zoological Society of London, 127: 545-553.
- STOROZHENKO, S. Y. 1996. New Upper Carboniferous grylloblattids (Insecta, Grylloblattida) from Siberia. Far Eastern Entomologist, 26: 18-20.
- STOROZHENKO, S. Y. 1998. Sistematika, filogeniya i evolyutsiya grilloblattidovykh nasekomykh (Insecta: Grylloblattida). Dal'auka, Vladivostok, Country, 207 pp.
- STOROZHENKO, S. Y. 2002. 2.2.2.2.1. Order Grylloblattida Walker, 1914 (=Notoptera, Crampton, 1915, =Grylloblattodea Brues et Melander, 1932, + Protorthoptera Handlirsch, 1906, = Paraplecoptera Martynov, 1925, + Protoperlaria Tillyard, 1928). In: History of Insects, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 278-281.
- VIGNON, P. 1929. Introduction à de nouvelles recherches de morphologie comparée sur l'aile des insectes. Archives du Muséum d'Histoire Naturelle, Paris, 4: 89-123.

- WHEELER, W. C., WHITING, M., WHEELER, Q. D. & CARPENTER, J. M. 2001a. The Phylogeny of the Extant Hexapod Orders. *Cladistics*, 17: 113-169.
- WHEELER, W. C., WHITING, M., WHEELER, Q. D. & CARPENTER, J. M. 2001b. Erratum. *Cladistics*, 17: 403-404.
- ZEUNER, F. E. 1939. Fossil Orthoptera Ensifera. British Museum (Natural History), London, Country, xiv + 321 + plates volume pp.
- WILLMANN, R. 1999. The Upper Carboniferous *Lithoneura lameeri* (Insecta, Ephemeroptera ?). *Paläontologische Zeitschrift*, 73: 289-302.
- ZHERIKHIN, V. V. 2002. 2.2.2.1.3. Order Mantida Latreille, 1802. The mantises (=Mantodea Burmeister, 1838). In: *History of Insects*, RASNITSYN, A. P. & QUICKE, D. L. J. (Eds), Kluwer Academic Publishers, Dordrecht, The Netherlands: 273-276.

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