

No evidence for Paleozoic origin of mantises (Dictyoptera: Mantina)

Нет свидетельств палеозойского происхождения богомоллов (Dictyoptera: Mantina)

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The hypothesis of Paleozoic origin of mantises recently proposed by Béthoux & Wieland is discussed. It is shown that these authors reject the logical scenario of evolution of the main higher taxa in the order Dictyoptera, well grounded by the morphological, paleontological and molecular data, in favor of the opposite one based on two very feeble assumptions: about inexplicable importance of one of the very common fusions of veins *RS* and *MA* in the tegmina of one of the Carboniferous polyneopterans, and about some traces of basal fusion of *RS* and *M* ostensibly present in the tegmina of recent mantises. Arguments against these views are considered.

Обсуждается гипотеза о палеозойском происхождении богомоллов, недавно выдвинутая Бету и Виландом. Показано, что эти авторы предлагают отвергнуть логичный сценарий эволюции высших таксонов отряда Dictyoptera, хорошо обоснованный морфологическими, палеонтологическими и молекулярными данными, в пользу противоположного сценария, основанного на двух очень слабых допущениях: о необъяснимой важности одного из очень обычных слияний жилок *RS* и *MA* в надкрыльях одного из карбоновых представителей Polyneoptera, и о каких-то следах базального слияния жилок *RS* и *M*, якобы присутствующих в надкрыльях современных богомоллов. Аргументы против этих взглядов приводятся.

Key words: recent and fossil mantises, eoblattids, taxonomy, wing venation, phylogenetic relations, Dictyoptera, Mantina, Eoblattida, Paleozoic, Carboniferous

Ключевые слова: современные и ископаемые богомоллы, эоблаттиды, таксономия, жилкование крыльев, филогенетические отношения, Dictyoptera, Mantina, Eoblattida, палеозой, карбон

INTRODUCTION

Recently a poor attempt to resurrect the obsolete idea about the Paleozoic age of mantises and independent development of mantises and cockroaches since the Carboniferous was made (Béthoux & Wieland, 2009). The previous hypothesis about the Paleozoic origin of mantises belongs to Handlirsch (1906–1908): he described the Paleozoic family “Palaeomantidae” (Palaeomanteidae) and included it in his “Ordnung Mantoidea” (the former order Mantodea). However, this opinion was persuasively re-

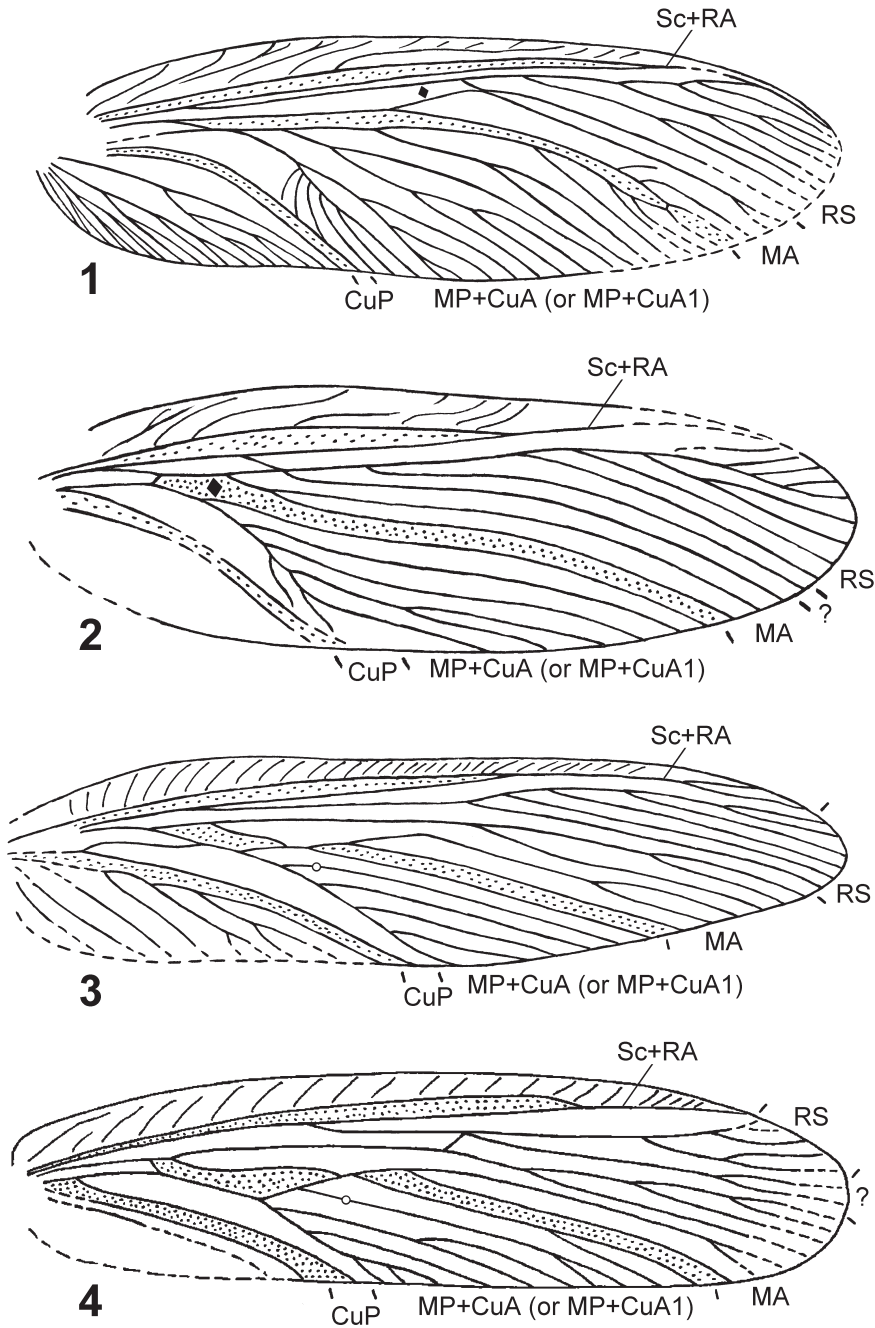
futed by Martynov (1927) who put this family in a separate order (Miomoptera inside Polyneoptera). Later, Rohdendorf (1977) and Rasnitsyn (1980) showed Miomoptera (=Paleomanteida) to be the most primitive order of Holometabola. Moreover, the recent morphological and molecular investigations (Klass, 1997; Maekawa et al., 1999; Beutel & Gorb, 2001; Whiting, 2002; Terry & Whiting, 2005; Kjer et al., 2006; Klass & Meier, 2006; Yager & Svenson, 2008) as well as paleontological data (Vršanský, 2002; Zherikhin, 2002; Grimaldi, 2003; Gorochov, 2006) convincingly show that mantises are

undoubtedly related to cockroaches, that these groups have many common synapomorphies, that the appearance and increase of differences between these groups in the second half of the Mesozoic are reflected in the paleontological record, and that these groups may therefore be included in the order Dictyoptera as two of its four suborders (these four suborders are the paraphyletic Mylacridina and Blattina, and the holophyletic Mantina and Termitina; Gorochov, 2001, 2004).

GENERAL VENATION OF TEGMINA

Béthoux & Wieland (2009) base their idea about the Carboniferous origin of mantises (Mantina) on the study of wings in some rather enigmatic Paleozoic insects (*Mesoptilus dolloi*, Upper Carboniferous; *Homocladus grandis*, Lower Permian) and of aberrant venation in some recent mantises. They found that the tegmina of the above-mentioned Paleozoic insects had a similarity to those of *Metallyticus splendidus* (a recent species of mantises) in the hind stem of *MP+CuA* with a rather dense comb of longitudinal branches [the names of veins in the paper by Béthoux & Wieland and in the present paper are not identical; here (see Figs 1–9), I use the nomenclature adapted for all the orders of Polyneoptera by Sharov (1962, 1968) and Gorochov (1995, 2004), since the nomenclature by Béthoux & Wieland is difficult to understand: the first coauthor designated the same vein as *CuA* in the cited paper and as *CuA+CuPaa* in some previous papers (Béthoux & Nel, 2001, 2002)]. However, in some other species of the same genus, these branches may be less numerous, and in the overwhelming majority of other recent mantises as well as in the oldest (fossil) true mantises, the hind branch of *MP+CuA* is single or bifurcate only (Figs 8, 9). Thus, the similarity in structure of *MP+CuA* in *Mesoptilus* and *Metallyticus* is the result of convergence, possibly connected with some widening of the tegmina in the latter genus.

Moreover, *Mesoptilus* has the same type of tegminal venation (including preservation of the distal fusion of *Sc* and *RA* stocks) as many typical representatives of the Paleozoic order Eoblattida (Figs 1–4). The tegminal venation of this genus (Fig. 2) is almost intermediate between that of the family Eoblattidae (Fig. 1) and that of the Carboniferous genus *Ischnoneura* (Fig. 3). The branches of *Sc* are partly longitudinal in *Mesoptilus* and *Eoblatta*, and a few characteristic additional veins between *CuP* and *MP+CuA* are developed in these genera [it is necessary to note that in some groups of Polyneoptera, the latter area contains a longitudinal vein usually treated as *CuA2*; it is not clear whether *CuA2* is lost among irregular crossveins in some other groups of Polyneoptera, or *CuA2* is merely a hind branch of *MP+CuA* with the base shifted more proximad than the place of fusion of *MP* and *CuA*]. However, *Mesoptilus* is similar to *Ischnoneura* and Cnemidolestidae (Figs 2–4) in a comb-like *MP+CuA* with rather numerous longitudinal branches situated on the hind stem (in *Eoblatta*, these branches are situated on the fore stem of *MP+CuA*; Fig. 1). Aristov (personal communication) also considers *Mesoptilus* related to *Ischoneura*; in one of his papers (in press), he included these genera in the Paleozoic order Hypoperlida, but now he inclines to my opinion about belonging of these genera to Eoblattida. *Ischnoneura* and Cnemidolestidae are undoubtedly related to one another, they are additionally similar in more transverse (than in *Mesoptilus* and *Eoblatta*) branches of the tegminal *Sc* and a short fusion of *MA* stock with the fore branch of *MP+CuA* (Figs 3, 4); in *Protodiamphipnoa* (Cnemidolestidae), translocation of one of the branches of *MP+CuA* from its hind stem to its fore stem is observed (Fig. 4). Thus, *Mesoptilus* may be placed near the base of the phylogenetic stock leading from *Eoblatta*-like ancestors to highly predaceous Cnemidolestidae. It is therefore not surprising that *Mesoptilus* had the raptorial type of fore legs (similar to that of *Ischnoneura*); it seems more surpris-



Figs 1–4. Tegmina of Eoblattida (schematically), Late Carboniferous: 1 – *Eoblatta robusta* (Brongniart); 2 – *Mesoptilus dolloi* Lamere; 3 – *Ischnoneura oustaleti* (Brongniart); 4 – *Protodiamphipnoa gaudryi* (Brongniart). Areas between *Sc* and *R*, between *MA* and *MP*, and between *CuP* and *1A* dotted; place of short fusion of *RS* stem with one of branches of *MA* in *M. dolloi* designated by small black diamond in tegmen of *E. robusta* (1); place of short fusion of *MA* stem with one of branches of *MP+CuA* in *I. oustaleti* and *P. gaudryi* designated by small black diamond in tegmen of *M. dolloi* (2); one of branches of *MP+CuA*, changing its position in *P. gaudryi*, designated by small circle in tegmen of *I. oustaleti* and of *P. gaudryi* (3, 4).

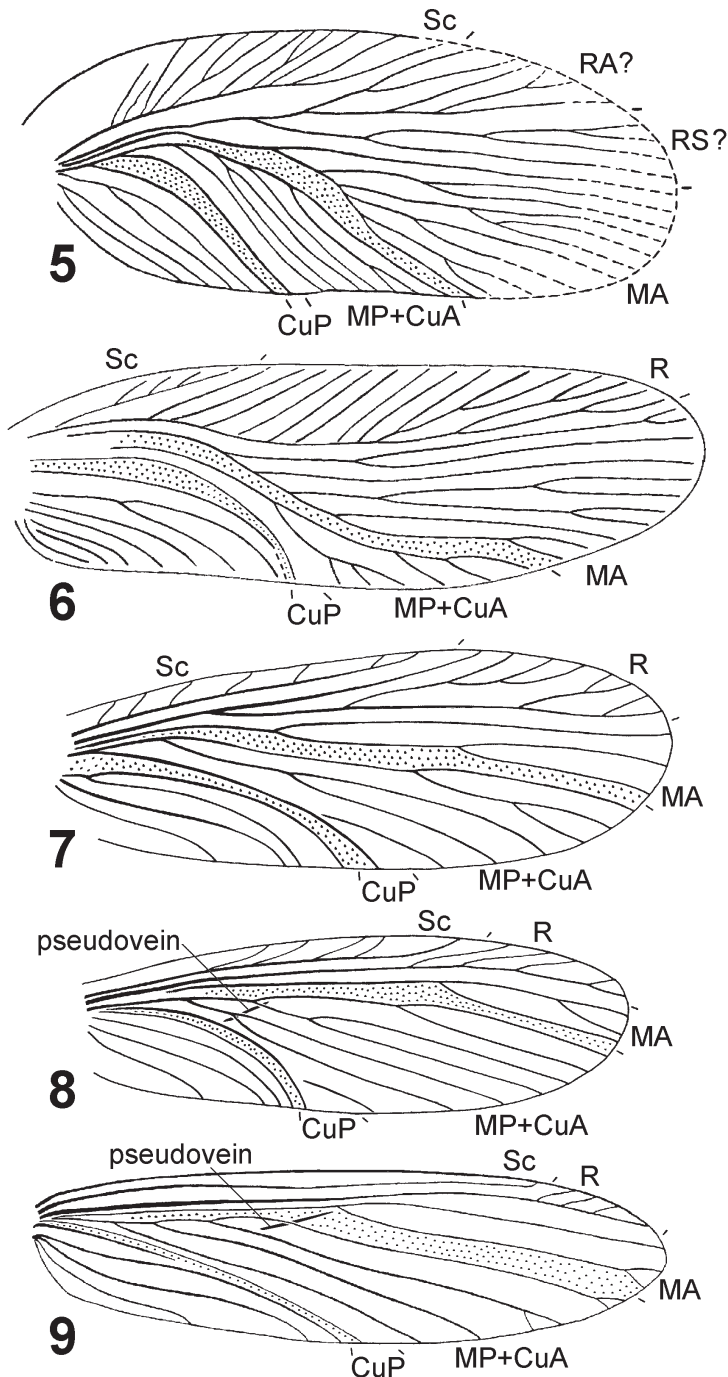
ing that Béthoux & Wieland did not include the latter family (having larger raptorial fore legs) in their Mantodea. It is necessary to note that the origin of raptorial legs in Cnemidolestidae and Mantina is evidently independent: in the Cnemidolestidae, these legs were with small coxae (typical of Polyneoptera), but the Dictyoptera (including mantises) has long coxae on all the legs (since the Middle Carboniferous, and only in some specialized recent termites, these coxae have been somewhat shortened). The tegminal venation of *Homocladus* (Béthoux et al., 2010) is also rather similar to that of *Mesoptilus* but distinguished mainly by the presence of more numerous branches of *RS*, *MA* and *MP+CuA*; thus, *Homocladus* is rather closely related to *Mesoptilus* and must also be included in the order Eoblattida.

Comparison of the tegminal venation in the mantises and in the oldest fossil cockroaches gives clearer evidence of their relationship. The fusion of the distal parts of *Sc* and *RA* is lost (this fusion is not visible in many representatives of the Middle Carboniferous Mylacridina; Fig. 5); the ancient division of *R* into two distinct stocks (*RA* and *RS*) is lost in the main phylogenetic branch of Dictyoptera (it is impossible to separate the branches of these stocks from each other in many of the Paleozoic and more recent dictyopterans; Figs 6–9); the proximal part of *MP* before its fusion with *CuA* (present in many polyneopterans and in some other ancient insects: Paoliidae and others) has disappeared, i.e. changed into a crossvein indistinguishable from the nearest crossveins (Figs 5–9). The separation of mantises from their cockroach-like ancestors was probably accompanied by some change in the function of tegmina: they began to participate in flight more actively than in cockroaches (in the latter insects, they mostly have a protective function) and to acquire costalization of their lateral (costal) part. An intermediate stage of this process is observed in the Lower Cretaceous genus *Baissomantis* (Fig. 7): *Sc* becomes longer; branches of *R* and *MA* become less

numerous and move towards the costal edge of the tegmina. In the oldest true mantises having a characteristic pseudovein (a thickened stripe of the wing membrane) in the tegmina, this process is continued: the few branches of *R* move towards the tegminal apex; the fore branches of *MP+CuA* move towards the costal edge (Fig. 8). In the majority of recent mantises, the number of *MA* branches in the tegmina is reduced to only two long branches, and the area between *R* and *MA* becomes very narrow; as shown by Gorochov (1995), numerous irregularities in the veins outlining such narrow areas are possible: translocations of branches from one stem to another (Figs 10, 11), different contacts and short fusions of veins (Figs 12–16). All of them are indicated for the recent mantises by Béthoux & Wieland, but these irregularities provide no evidence of the fusion of *RS* with *M* in a general ancestor of mantises and evidence of the “Carboniferous origin” of this ancestor.

THE PROBLEMS OF FUSION OF VEINS *RS* AND *M*

One of the main reasons for uniting mantises with the Paleozoic Eoblattida but not with the Mesozoic cockroaches is the hypothesis by Béthoux & Wieland (2009) about the fusion of *RS* and *M* at the tegminal base of mantises. However, *Mesoptilus* has the base of *RS* almost in the middle part of tegmina, i.e. approximately at the same place as in many other polyneopterans (including Eoblattida and the Middle Carboniferous cockroaches; Figs 1–5); its *RS* is in contact or shortly fused with one of branches (or with one of the stems) of *MA* but not with the more proximal part of *M*; and this fusion in *Mesoptilus* is located near the base of *RS* but not at the tegminal base. In *Eoblatta*, there is a similar contact (almost a fusion) between the proximal part of the hind branch of *RS* and one of *MA* branches; this contact is located not far from the place of a similar fusion in *Mesoptilus* (Fig. 1). What, then, is the reason to include only *Mesop-*



Figs 5–9. Tegmina of Dictyoptera (schematically): 5 – *Grypoblattides flabellatus* Becker-Migdisova (Mylacridina), Middle Carboniferous; 6 – *Gurvanoblatta mongolica* Vishniakova (Blattina), Early Cretaceous; 7 – *Baissomantis maculata* Gratshev et Zherikhin (Mantina?), Early Cretaceous; 8 – *Cretophotina tristriata* Gratshev et Zherikhin (Mantina), Early Cretaceous; 9 – *Chaeteesa filata* Burmeister (Mantina), recent. Areas MA–MP и CuP–1A dotted; pseudovein – thickened tegminal stripe characteristic for true mantises.

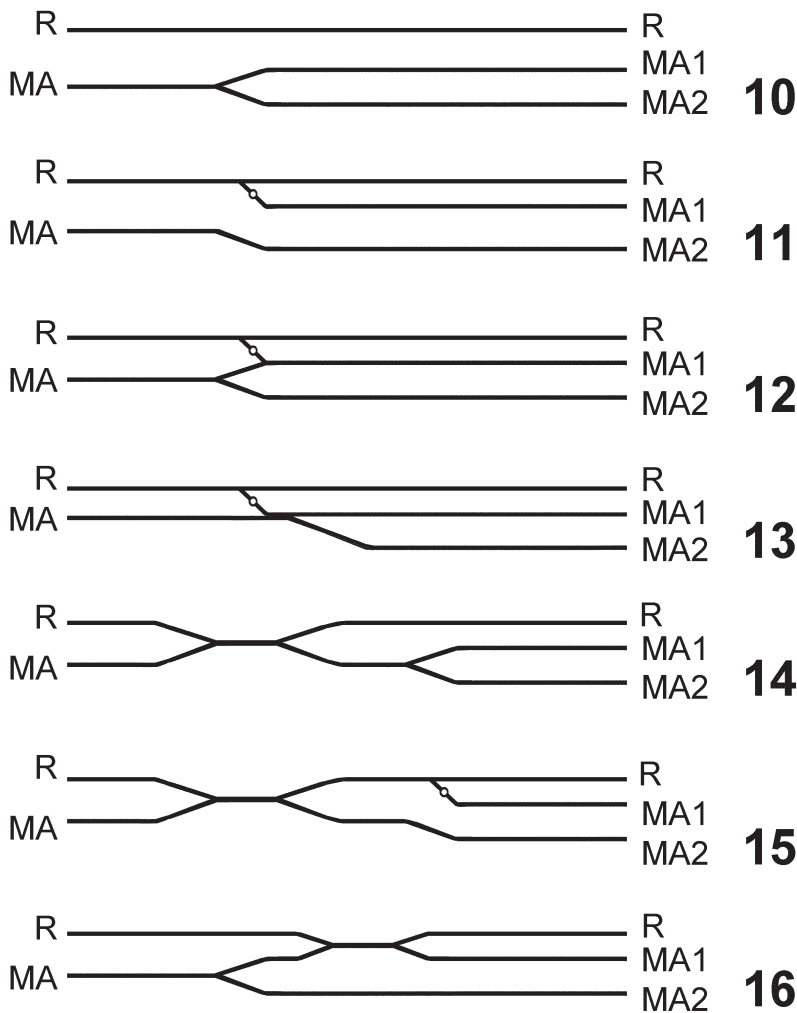
tilus and *Homocladus* (for *Homocladus*, the presence of such fusion is very not evident) but not *Eoblatta* in Mantodea? Such fusions, as shown by the above and pictured by the coauthors for recent mantises, appear very often and cannot in any way justify a radical change in the system of our knowledge about the evolution of Dictyoptera.

Another problem is the “discovery” of possible traces of possible fusion of *RS* and *M* in the tegminal base of recent mantises. I examined the numerous specimens of different mantises from the collection of the Zoological Institute (Russian Academy of Sciences) and could not find any plausible trace of this fusion. Moreover, the coauthors published only a few indistinct photographs of these traces. Designations on these photographs are also not clear enough. No any schematic explanation of these enigmatic pictures is offered. The basal parts of main veins in the tegmina of recent mantises and cockroaches are very similar (Figs 17, 18), but these parts form a rather complicated apparatus for the articulation with the thorax; this apparatus includes some additional sclerotizations of areas between the veins, which may secondarily connect some veins. If someone wished very much to find formal support of his feeble hypotheses about different fusions of veins, he would certainly be able to interpret these additional sclerotizations, pseudoveins or modified basal crossveins as traces of proximal fusion of *RS* and *M*, of *M* and *CuA* (Béthoux & Nel, 2001), or of other veins.

OTHER MORPHOLOGICAL AND MOLECULAR DATA

Morphology of other body structures (besides wings) also shows significant similarity and relationship between recent cockroaches and mantises [similarity in their fossil wings is demonstrated by Vrsanski (2002), Zherikhin (2002) and Grimaldi (2003)]: common synapomorphies are numerous, from the perforated tentorium and long coxae of legs to the characteristic

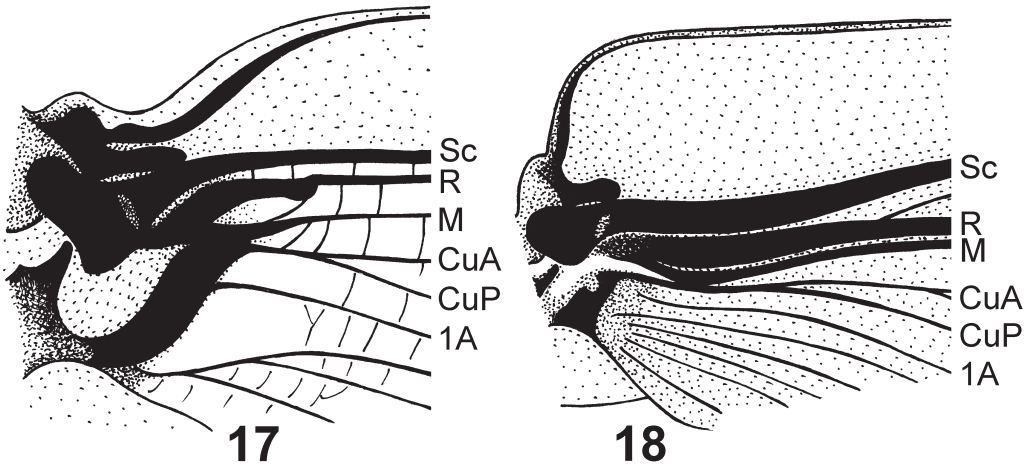
construction of genitalia and of some other structures (Klass, 1997; Beutel & Gorb, 2001; Gorochov, 2001, 2006; Klass & Meier, 2006; Yager & Svenson, 2008). The genital similarity is the most important. The male genitalia of Blattina and Mantina are very similar; their general asymmetric shape, the mode of function during copulation, and almost the same sclerotized elements (many of which are very similar and clearly interpreted as homologous structures; Klass, 1997) provide us almost direct evidence of their not very ancient divergence. In all the other orders of Polyneoptera, male genitalia with clearly homologous complicated sclerotized structures are characteristic of groups that diverged from each other not earlier than the Jurassic or Early Cretaceous: different subfamilies of the family Gryllidae (this family is unknown before Early Cretaceous; the nearest families Gryllotalpidae and Mogoplistidae have a similar age and acquired sclerotized elements in their complicated genitalia independently from Gryllidae and from one another; all these families have non-homologous sclerotized elements in the male genitalia), different groups of the superfamily Acridoidea (this superfamily is unknown in Mesozoic, and its oldest taxa possibly diverged from each other only in Paleogene), all the recent groups of Dermaptera with homologous sclerotized structures are known only since Early Cretaceous (the Late Jurassic representatives of Dermaptera belong to some more primitive groups with unknown structure of male genitalia). Also, in all the polyneopteran orders having complicated male genitalia and known since the Paleozoic, sclerites of such genitalia are absolutely non-homologous to those of any other orders. The “genital clock” hypothesis (Gorochov, 2005) based on these facts assumes that changes in the complicated male genitalia more or less follow the genetic drift and that preservation of the same type of such genitalia is possible for 100–150 million years but not for 250–300 million years. Many other morphological synapomorphies



Figs 10–16. Normal (10) and aberrant (11–16) variants of venation in narrow part of area between *R* and *MA* in mantises (schematically): 11, translocation of anterior branch of *MA* to *R* [compare with Fig. 16 C in Béthoux & Wieland (2009)]; 12, intermediate variant between normal and previous variants [compare with Fig. 16 D in same paper]; 13, short fusion of anterior branch of *MA* (after translocation to *R*) with posterior branch of *MA* [compare with Fig. 16 G from same paper]; 14, short fusion of *R* stem with *MA* stem [compare with Figs 1 A, B in same paper]; 15, same fusion and translocation of anterior branch of *MA* to *R* [compare with Fig. 5 E in same paper]; 16, short fusion of *R* stem with anterior branch of *MA* [compare with Fig. 10 D in same paper].

of the recent mantises and cockroaches (+ termites) also clearly unite these groups in a separate monophyletic taxon; but for all the other polyneopteran orders of Paleozoic origin, establishment of phylogenetic relations is a very difficult problem. Molecular phylogenetic studies also establish a more

or less stable relationship of mantises and other Dictyoptera but give very controversial results for the phylogenetic connections of other orders of Polyneoptera (Maekawa et al., 1999; Whiting, 2002; Terry & Whiting, 2005; Kjer et al., 2006). This situation with the morphological and molecular data



Figs 17, 18. Venation of basal part of tegmina in Dictyoptera (schematically): 17 – *Tenodera* sp. (Mantina); 18 – *Rhabdoblatta* sp. (Blattina). Semiclerotized areas dotted.

may be understood, if we assume that divergence of mantises and recent cockroaches began after a long period of accumulation of future morphological and molecular synapomorphies in their common ancestors from the Carboniferous to the middle of the Mesozoic. However, most polyneopteran orders diverged from each other in rather short time (rapid adaptive radiation) in the Carboniferous; this short period allowed them to accumulate only a few common characters which may have been lost during the long subsequent evolution or may be omitted in the phylogenetic study.

Thus, Béthoux & Wieland propose to reject this logical and understandable scenario, well grounded by morphological, paleontological and molecular data, in favor of the opposite one based on two very feeble assumptions: about inexplicable importance of one of the very common fusions of *RS* with *MA* in the tegmina of one of the Carboniferous polyneopterans (*Mesoptilus*), and about some traces of the basal fusion of *RS* and *M* ostensibly present (but really invisible) in the tegmina of recent mantises. Finally, it is useful to write about a status of feeble hypotheses. I think that such hypotheses are suitable if one tries to interpret some new and obscure facts lack-

ing any other explanation and if one's feeble hypotheses do not disturb any other hypotheses based on other facts (and certainly, such feeble hypothesis must not be any reason for great changes in classification of higher taxa and in nomenclature of veins or other structures). For example, I proposed a feeble hypothesis about possible related connections of the new family Alexarasniidae (Gorochov, 2011) because this hypothesis does not disturb any more elaborated recent hypothesis about the possible ancestors of the family Chresmodidae. However, if a new hypothesis rejects the previous one, its author should discuss all the facts used by the opponents, and propose a new explanation for these facts. If the new hypothesis embraces more numerous facts and organizes them in a less contradictory scenario, it has the right to exist. In the opposite case, such a hypothesis will appear amateurish.

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