Early Mecopterida and the systematic position of the Microptysmatidae (Insecta: Endopterygota)

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Abstract. In recent times many authors have regarded the Protomeropidae and Microptysmatidae - two essentially Permian groups - as either early trichopteran lineages or members of the stem-group of the Amphiesmenoptera (basically: Trichoptera + Lepidoptera). Actually none of these families possesses, in its ground plan, the most significant derived trait of the amphiesmenopteran forewing, namely a true 'double-Y loop' arrangement of the anal veins. Since 'Carpenter's organs', small rounded structures in the costal area of the hindwing, are only known to occur in certain members of the Permochoristidae, Kaltanidae and Protomeropidae, these three families should belong to a fossil clade, which we ascribe to the Mecoptera, suborder Pistillifera *sensu lato*, mainly on account of a few venational features. Although we maintain the Microptysmatidae in the Mecopterida (= Panorpida, i.e. Amphiesmenoptera, Mecoptera, Diptera, and relatives), we propose to place this family in a separate order: the **Permotrichoptera**, **n. status**. Indeed, apparently, Microptysmatidae can be ascribed neither to the Amphiesmenoptera nor to the Antliophora (= Mecoptera-Diptera complex).

Résumé. Les premiers Mécoptéroïdes et la position systématique des Microptysmatidae (Insecta : Endopterygota). Dans une période relativement récente, de nombreux auteurs ont considéré Protomeropidae et Microptysmatidae - deux groupes essentiellement permiens - soit comme des Trichoptera archaïques, soit comme des éléments du « groupe-racine » des Amphiesmenoptera (fondamentalement : Trichoptera + Lepidoptera). En fait, aucune de ces familles ne possède, dans son plan de base, la principale apomorphie de l'aile antérieure des Amphiesmenoptera, à savoir la boucle caractéristique, en « double Y », formée par les nervures anales. Dans la mesure où les « organes de Carpenter » (petites structures arrondies du champ costal de l'aile postérieure) ne sont signalés que chez certains Permochoristidae, Kaltanidae et Protomeropidae, ces trois familles doivent appartenir à un clade fossile que nous attribuons aux Mecoptera, plus précisément au sous-ordre des Pistillifera *sensu lato*, avant tout en fonction de caractères de la nervation alaire. Bien que nous maintenions les Microptysmatidae dans les Mécoptéroïdes (= Panorpoïdes : Amphiesmenoptera, Mecoptera, Diptera et taxons apparentés), nous proposons de ranger cette famille dans un ordre à part : les Permotrichoptera, n. status. En effet, les Microptysmatidae ne semblent pouvoir être attribués ni aux Amphiesmenoptera, ni aux Antliophora (= complexe « Mecoptera-Diptera »).

Keywords: Amphiesmenoptera, Antliophora, fossil Mecoptera, Permotrichoptera, Holometabola.

The recently discovered Jurassic insect fauna from the Jiulongshan Formation is situated in the autonomous region of Inner Mongolia (China). These fossil insects are considerably diverse with a number of undescribed specimens attributable to the Amphiesmenoptera. In order to be able to study the characters and systematic placement of these species in forthcoming papers, we considered useful and necessary to reexamine the definition and composition of the earliest amphiesmenopteran lineages. Indeed, it became soon obvious that certain fossil taxa (Riek 1970: fig. 8.21), mostly of Permian age, had to be excluded from the Amphiesmenoptera and transferred to the Mecoptera (a systematic position already widely accepted in 'precladistic' times) or to the Permotrichoptera, a mecopteroid group here raised to ordinal rank.

Material and methods

Through comparative examination of the basalmost taxa in every extant order of Endopterygota on the one hand (= Holometabola; material kept in the Muséum National d'Histoire Naturelle, Paris), of the earliest endopterygote fossils on the other hand (taking notably account of such excellent works as Novokshonov 1997; Rasnitsyn & Quicke, eds 2002; Grimaldi & Engel 2005), an attempt was made at reassessing the polarity of several imaginal characters (from wings and legs), some of which had been neglected in previous cladistic literature (e.g. pretarsal claw morphology in Mecoptera). These outgroup comparisons were

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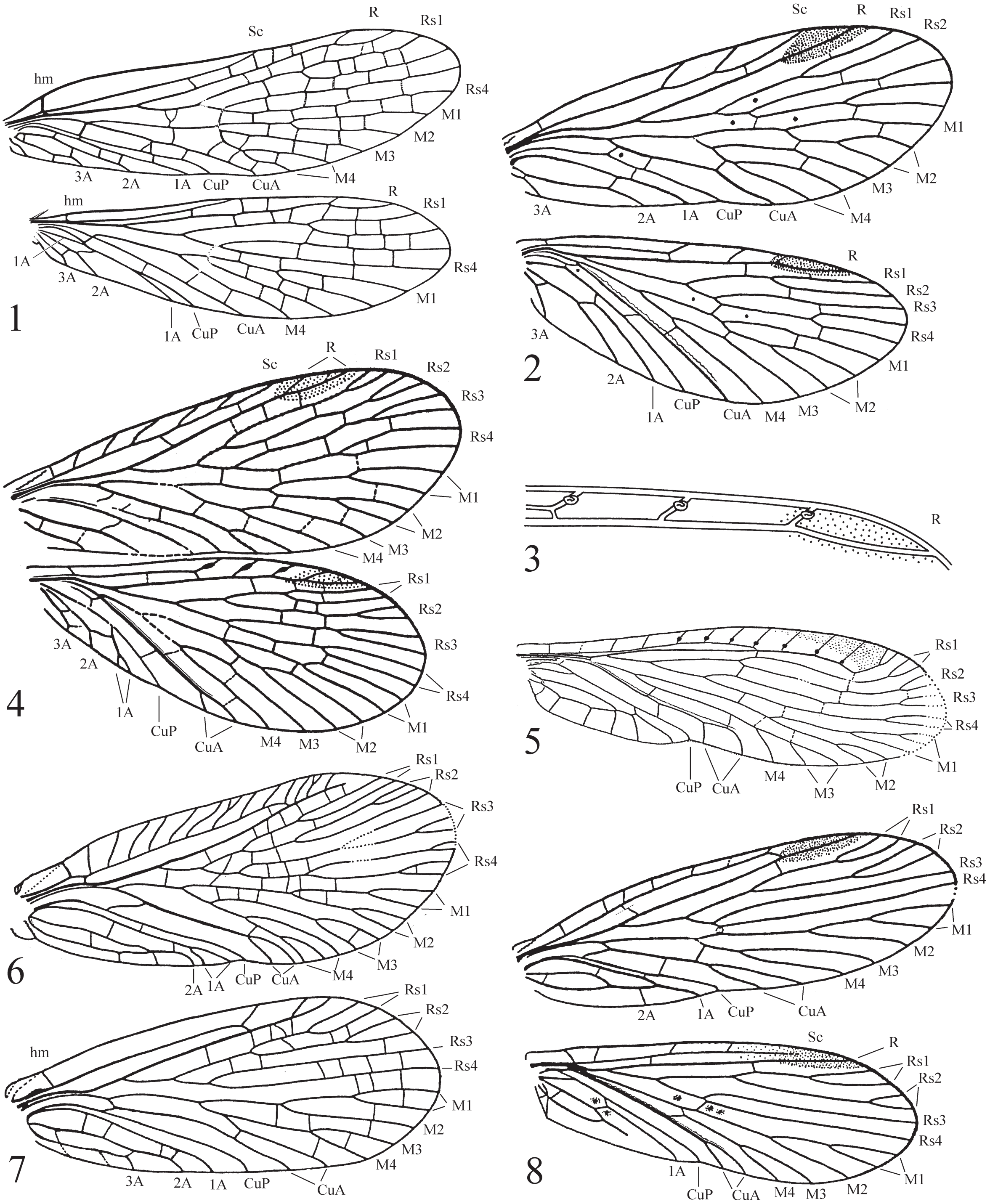

Figures 1–8
Mecoptera (1–6) and Permotrichoptera (7–8), Recent (1) / fossil (2–8) taxa: wing venation (1, 2, 4–8) and part of hindwing with Carpenter's organs (3). **1**, *Meridiochorista ruficeps* (Newman 1850), Choristidae; **2** and **3**, *Agetopanorpa sp.* (2: ♀ – 3: ♂), Permochoristidae; **4**, *Altajopanorpa pilosa* (Martynova 1958) (♂), Kaltanidae; **5**, *Permomerope ramosa* Sukatsheva 1976 (♂ hindwing), Protomeropidae; **6**, *Pseudomerope oborana* Kukalová-Peck & Willmann 1990 (holotype, forewing), Protomeropidae; **7**, *Microptysmella moravica* Kukalová-Peck & Willmann 1990 (holotype, forewing), Microptysmatidae; **8**, *Kamopanorpa pritykinae* (Sukatsheva 1976), Microptysmatidae. Modified from Kukalová-Peck & Willmann (1990) (6, 7), Novokshonov (1997) (2–5; 8), and Willmann (1989) (1) [different magnifications].

carried out within the framework of our current knowledge of the phylogeny of the Recent Endopterygota (Kristensen 1999; Whiting 2004; Terry & Whiting 2005; Beutel & Pohl 2006; Krenn 2007), Hymenoptera (Schulmeister 2003; Sharkey 2007), Amphiesmenoptera (Wiegmann *et al.* 2002; Holzenthal *et al.* 2007; Kristensen *et al.* 2007), and Mecoptera (Willmann 1989; Whiting 2002, 2004; Grimaldi & Engel 2005). It is to be noted that we do not regard the order Strepsiptera as a member of the Antliophora (Kristensen 1995; Beutel & Gorb 2001; Grimaldi & Engel 2005; Bonneton *et al.* 2006; Wiegmann *et al.* 2009a, b), and do not accept the recently proposed (Beutel & Baum 2008) 'possible clade' that would gather Siphonaptera, Nannomecoptera and Diptera. Indeed the latter hypothesis is based on adult head morphology but gets no further support from larval head morphology (Beutel *et al.* 2009: 457) and is really at variance with published molecular studies (Whiting 2002; Wiegmann *et al.* 2009b).

Results and discussion

1. Wing venation

1.1. Terminology.

In recently published papers (e.g. Kukalová-Peck 1991; Kukalová-Peck & Lawrence 2004), certain authors consider that the proximal section of the 'media anterior' (MA) is entirely merged with the stem of the radius (R) in the Eumetabola (= Paraneoptera + Endopterygota) and part of the lower Neoptera. Accordingly they call "RP + MA" the radial sector (Rs) of Comstock (1918). However, this theory is not supported by indisputable evidence and is seriously contradicted by the interpretation of the venation based on homologies with the wing tracheation in many nymphs (e.g. Comstock 1918: figs 270–272) and pupae (e.g. text-figs 1–3 in Tillyard 1919a). We will thus follow the classical nomenclature (Comstock 1918; Wootton 1979; Kristensen 2003) for insect wing veins and retain Tillyard's (1919a, b) designations for the main crossveins present in the Mecopterida, not for the alleged base of 'M5' however (Tillyard 1919b: text-fig. 38): in fact a mere crossvein, which is often strongly oblique (Kukalová-Peck & Willmann 1990: fig. 1, ST).

1.2. Remarks about certain veins.

Forewing subcostal crossveins. In the forewing of most Neuropterida, there are several (often many) crossveins between the costa and vein Sc, distad of the humeral crossvein (hm). This condition, which probably corresponds to a plesiomorphy of the endopterygote ground plan (such crossveins can be considered remnants of the archedictyon), is also known to occur in the Glosselytrodea (Grimaldi & Engel 2005: fig. 9.2), certain "Miomoptera" (e.g. *Permosialis* Martynov 1928), the "Cladochoristidae" and certain Microptysmatidae (Fig. 8). In the forewing ground plan of the Mecoptera, there seems to be at most two subcostal crossveins distad of hm (fossil Nannochoristidae) (see in Novokshonov 1997: figs 39–40; Grimaldi & Engel 2005: fig. 12.10) if one takes into account on the one hand the basal position of the Nannochoristidae within the order, on the other hand the absence of these crossveins in the Diptera (sister to Mecoptera among extant insects). The presence of more subcostal crossveins in certain extant (e.g. Meropeidae) or extinct (Figs 4, 6) Mecoptera may thus correspond to a reversal, as already suggested for three extant lineages by Willmann (1989: fig. 113).

Number of Rs branches. A four-branched Rs, as normally observed in the Amphiesmenoptera (that never possess more branches), also occurs in certain Miomoptera (Rohdendorf ed. 1962: figs 364–365), a few primitive Neuropterida (e.g. the megalopteran species *Stenosialis* Tillyard 1919, and the raphidiopteran species *Metaraphidia vahldieki* Willmann 1994) (Rasnitsyn & Quicke eds 2002: fig. 240, where 'MA' is in fact Rs3+4), many Mecoptera (Fig. 1), including the fossil nannochoristid genus *Itaphlebia* Sukatsheva 1985 (see figs in Novokshonov 1997), etc. This trait indisputably pertains to the ground plan of the Endopterygota, as well as to that of the Mecoptera. Through homoplasy, several endopterygote insects have evolved a forewing with additional Rs branches (Figs 2 and 4–8).

Number of M branches in the forewing. A four-branched M can be ascribed to the ground plan of the Eumetabola: it occurs in the basalmost Psocodea (Rohdendorf ed. 1962: figs 678, 679, 681 and 699), several Hemiptera (e.g. typical Cicadidae), certain Megaloptera (Glorioso 1981: figs 16 and 17; Theischinger 1991: fig. 32.5B), a fossil Raphidioptera (*Nanoraphidia*, see Engel (2002)), the Nannomecoptera (Nannochoristidae), many Amphiesmenoptera (including fossils, such as *Eocorona iani* Tindale, 1980), etc. Contrary to what is sometimes assumed, the presence of more than four M branches in various groups of Endopterygota should not be regarded as a symplesiomorphy. In particular, the divided vein M4 occurring in several extant (Fig. 1) or extinct (Figs 2, 6) Mecoptera is a synapomorphy that does not belong to the ground plan of this order (contrary to Willmann's (1989) opinion – see farther on: section 7).

Vein CuA. Kukalová-Peck & Willmann (1990), in the original description of the monotypic genus *Microptysmella* (Microptysmatidae), interpret as M4 ('MP4') the vein that we regard as CuA1 (Fig. 7: CuA, upper branch). Accordingly, since they view microptysmatids – tentatively – as an early amphiesmenopteran lineage, they ascribe a simple (i.e. unforked) CuA not only to the ground plan of the Antliophora, but also to that of the Amphiesmenoptera (in spite of the distinctly two-branched CuA present in most Trichoptera and Lepidoptera). For similar reasons, Willmann (1989: fig. 14) already listed a forked vein CuA ('Cu1') among the amphiesmenopteran autapomorphies, and a simple CuA among the synapomorphies of the Antliophora and Amphiesmenoptera. If we regard, like Willmann, the forked CuA as a groundplan trait of the Endopterygota (clearly present in, e.g., the Megaloptera), we disagree with him about the evolution of this character within the Mecopterida, considering symplesiomorphic the forked CuA of the amphiesmenopterans, and autapomorphic the basically simple CuA of the Antliophora (the divided CuA of certain Mecoptera (Figs 4–6; Mickoleit 1971: fig. 10) must be of secondary origin, resulting from an increase in the number of wing vein branches). Indeed, as stated hereafter, Microptysmatidae should not be ascribed to the Amphiesmenoptera; moreover, their CuA is distinctly two-branched in most cases (Fig. 8: fore- and hindwings) and, in fact, also possesses two branches in *Microptysmella* (Fig. 7) whose venation is of the same type but shows a strongly oblique m-cu crossvein (exactly as in *Microptysma sibiricum* Martynova 1958: fig. 106 in Hennig 1981).

Forewing anal veins. These veins form a characteristic "double-Y" loop in Trichoptera and basalmost Lepidoptera. Typically the double-Y configuration can be described as two adjacent loops: a short lower one (undivided, with regularly arched ventral edge) and a large upper one, primarily crossed by a single veinlet (above the short loop). Occasionally, a short spur arises from the distal arched section of the lower edge of the large loop (Issiki [1954], fig. 12; Kristensen 1997: fig. 10): this spur, which does not reach the wing inner margin, corresponds to the apex of vein 2A and shows that the lower edge in question is composed of two parts, namely a section of 2A and a distal, typically oblique crossvein (Kristensen 2003: 87). This well defined 'double-Y' loop is the most reliable apomorphy for assigning a fossil insect to the Amphiesmenoptera (see section 6). Although most Microptysmatidae have a roughly similar double loop (nevertheless with vein 2A reaching inner wing margin: Fig. 8), the microptysmatid genus *Microptysmella* (Fig. 7) shows a fairly different arrangement of its anal veins: 2A reaches the wing margin and is connected to 1A by four crossveins, none of which is distinctly oblique so that there is no well defined upper loop. In fact, in this genus, the arrangement of the forewing anal veins does not differ significantly from that one can observe in certain Mecoptera (Fig. 1) und a number of Neuropterida (Theischinger 1991: fig. 32.5B; Novokshonov 2004: pl. 12, fig. 1). Several Protomeropidae also clearly lack a true 'upper loop' (Fig. 6) and have a 2A vein which reaches the wing margin. Therefore both Microptysmatidae and Protomeropidae have to be excluded from the superorder Amphiesmenoptera.

2. Nygmata

The nygmata are small thickened spots found on the wings of a number of endopterygote insects. Although sometimes regarded as "presumed sensory spots" (Nichols *et al.* 1989; New 1991: 527), they are more probably glandular structures in consideration of the appearance of certain of their cells (Brues 1933; Jolivet 1955; Kristensen 1989). They occur in several fossils and, among Recent taxa (Brues 1933; Jolivet 1955; Kristensen 1989; Byers 1991; Neboiss 1991; New 1991; Kukalová-Peck & Lawrence 2004; Holzenthal *et al.* 2007), in the Corydalidae (Megaloptera), certain Neuroptera and Mecoptera, most Trichoptera and many 'symphytan' Hymenoptera (for the Xyelidae: Macroxyelinae see figs in Shinohara (1992), and Smith & Schiff (1998)). The three nygmata observable on a nannochoristid wing (Kristensen 1989; Byers 1991; Grimaldi & Engel 2005) also occur, in identical positions, in – e.g. – the Panorpidae (Jolivet 1955) and can be reliably ascribed to the mecopteran ground plan. Two of these three nygmata, which lie in the Rs-M interspace (one near the first fork of M, the second one farther distad: Fig. 2), are clearly homologous with similarly situated nygmata in the Corydalidae and Xyelidae. Taking account of the basal position of these groups within the major endopterygote lineages (Kristensen 1999; Terry & Whiting 2005; Beutel & Pohl 2006; Sharkey 2007), viz. the Neuropterida + Coleoptera, Hymenoptera and Mecopterida, we tentatively regard these two nygmata as groundplan autapomorphies of the Endopterygota. Absence of these two nygmata in the Trichoptera and Lepidoptera (apparently also in all fossil amphiesmenopterans) can thus be considered secondary and may provide a further apomorphy for the definition of the Amphiesmenoptera. It should be noted that the proximal nygma of the trichopteran forewing was inappropriately called 'thyridium' by Holzenthal *et al.* (2007: 650): indeed, the term thyridium usually refers to a hyaline spot on the first fork of the media (Kristensen 1989; Nichols *et al.* 1989).

3. Carpenter's organs

In his redescription of the fossil species *Platychorista* *venosa* Tillyard 1926 (Protomeropidae), Carpenter (1930) noticed the existence of four 'small circular eye-spots' in the hindwing 'costal space, including the pterostigmatic area'. These structures, which are now known as 'Carpenter's organs' (Novokshonov 1997; Rasnitsyn & Quicke eds 2002: fig. 269), occur only in a few fossil insects, in which they apparently represent secondary sexual characteristics of the male (Figs 3–5): according to Novokshonov (2004: fig. 5), Carpenter's reconstitution of a female *Platychorista venosa* would in fact include, erroneously, at least part of a male hindwing (Carpenter 1930: pl. 4). Typical Carpenter's organs can be described as small circular spots of the hindwing observable on the apical section of Sc, on one/several branch(es) of R, and sometimes (Fig. 5) also on several other branches of Sc.

4. Tibial spurs

Ivanov (2002: 283: third group of synapomorphies) regards the presence of 'subapical' (= pre-apical, = medial) tibial spurs as a synapomorphy of the Microptysmatidae, Trichoptera (*s. str.*), and Lepidoptera. In fact, medial tibial spurs, often erroneously called 'spines', also occur in several basal lineages of the Hymenoptera, such as the Xyelidae (Smith & Schiff 1998), Pamphiliidae (fig. 69 in Richards 1956), and Cephidae with some instability in the number of pre-apical spurs (Benson 1946: 91). Given the paraphyletic nature of the 'Symphyta' (Schulmeister 2003; Sharkey 2007), three pairs of spurs (including the apical pair) can be ascribed to the hymenopteran ground plan, at least for the hindleg. In the Amphiesmenoptera, two pairs of tibial spurs is the normal complement for the hindleg and medial spurs sometimes also occur on other legs (notably in Trichoptera). Therefore, if one takes into account what is currently known about endopterygote phylogeny on the one hand, the absence of medial spurs in all exopterygote orders on the other hand, the presence of medial (or pre-apical) tibial spurs on one or more pair(s) of legs should be regarded as a synapomorphy of the Hymenoptera and Mecopterida, nevertheless secondarily lost (reversal) in the Antliophora.

5. Pretarsal claws

Up to now, little attention has been paid to the comparative study of mecopteran claws, even though conspicuously pectinate claws are present in the Panorpidae (Ferris & Rees 1939: fig. 48; Röder 1986: fig. 15c; Cai *et al.* 2008: 43). According to Byers (1991: 697–698), pectinate claws also occur in the Choristidae and the meropeid genus *Austromerope* Killington 1933, but not in the Australian Nannochoristidae (whose claw would possess a single basal tooth). Simple claws – well developed but without teeth – occur in Boreidae, Siphonaptera (Beutel & Gorb 2001), *Merope tuber* Newman 1838 (Meropeidae: Mickoleit 1967: 330), Apteropanorpidae (Byers 1991), Bittacidae, and Panorpodidae. In *Notiothauma reedi* MacLachlan 1877 (Eomeropidae), the proximo-median part of the ventral edge of the claw is provided with minute, though distinct teeth (Mickoleit 1971: fig. 8). Actually we have noticed the presence of at least three strong teeth on the ventral edge of the claw (proximo-median region) in a Chilean specimen of *Nannochorista neotropica* Navás 1928. Since Nannochoristidae are either the basalmost mecopteran lineage (Willmann 1987; Whiting 2004) or part of the basalmost mecopteran lineage (Whiting 2002; Grimaldi & Engel 2005), we regard the presence of a few well developed teeth in the median/proximo-median region of the claw as a previously unnoticed autapomorphy of the order Mecoptera. Secondary reduction (Eomeropidae) or loss of the teeth took place in several groups of Mecoptera, in particular in Boreidae + Siphonaptera (synapomorphy). In Diptera (McAlpine *et al.* eds 1981) and Amphiesmenoptera, the pretarsal claws are, typically, either simple or provided with a single tooth. Obviously, claw morphology remains to be investigated in fossil Mecopterida.

6. Fossil Amphiesmenoptera

The earliest genuine amphiesmenopteran lineage is the Permian-Triassic family Cladochoristidae. In fact, it probably constitutes a paraphyletic group. Indeed, except for the typical "double-Y" loop defined by its anal veins (Riek 1953, 1955; Willmann 1989: fig. 40d-e; Novokshonov 1993a: fig. 4b), its forewing venation does not really differ from the ground plan that we consider for the Endopterygota: presence of rather numerous crossveins between C and Sc (more than two beyond hm), Rs four-branched, M also with four branches, CuA two-branched, CuP with a single branch. Incidentally it should be noted that these plesiomorphic traits also occur in e.g. *Austrosialis* Tillyard 1919 (Megaloptera), a relatively basal neuropteroid genus whose forewing venation was already compared by Tillyard (1919b: text-fig. 47a-b) with the largely similar venation (symplesiomorphy) of a 'primitive' caddisfly (Trichoptera). The other fossil Amphiesmenoptera (with true 'double-Y' anal loop) that are neither trichopteran, nor lepidopteran, are the Triassic Eocoronidae (Tindale 1980: fig. 4), the Triassic-Jurassic Prorhyacophilidae (Riek 1955; Ansorge 2002, who regards *Prorhyacophila* Riek 1955 as a synonym of *Mesotrichopteridium* Handlirsch 1906), and the Mesozoic Necrotauliidae *sensu lato*, a paraphyletic assemblage in all probability (Sukatsheva 1968; Ivanov 2002; Ansorge 2002 (Necrotauliidae *sensu stricto*); Grimaldi & Engel 2005). Like the Trichoptera and Lepidoptera, these last three families have retained few, if any, subcostal crossveins in the forewing. While the eocoronid hindwing distinctly possesses four M veins (plesiomorphy), Prorhyacophilidae, Necrotauliidae, Trichoptera and Lepidoptera share a previously unnoticed synapomorphy, namely a hindwing media with at most three branches (M3 and M4 being entirely merged together, except in rare instances of teratological hindwings: figs 6F and 4.23 B in, respectively, Ansorge 2002 and Kristensen 2003).

7. Protomeropidae and their relatives

The Protomeropina Sukatsheva 1980 were initially proposed (Sukatsheva 1980) as a fossil suborder of the Trichoptera gathering the Cladochoristidae, Protomeropidae, Prosepididontidae, and Microptysmatidae. In fact, this group is definitely polyphyletic and none of these four families can be ascribed to the Trichoptera. The Prosepididontidae have been synonymized with the Geinitziidae and convincingly excluded from the Endopterygota (Ansorge & Rasnitsyn 2000). As mentioned in the above section, the 'Cladochoristidae' are early Amphiesmenoptera that differ from the other groups of this superorder in retaining more than two subcostal crossveins in the forewing, distad of the humeral crossvein (in Trichoptera and Lepidoptera, the – secondary – presence of many subcostal crossveins is exceptional and restricted to a few non-basal taxa: e.g. Neboiss 1991: fig. 40.10A). Like Microptysmatidae (see sections 1.2 and 8), the family Protomeropidae (= Platychoristidae, = Permomeropidae) cannot belong to the Amphiesmenoptera since its forewing ground plan lacks a genuine double-Y anal loop (Fig. 6). In the recent literature, the Protomeropidae are regarded either as amphiesmenopterans (even, sometimes, as trichopterans: e.g. Sukatsheva *et al.* 2007) or just as 'mecopteroid-like' insects (Kukalová-Peck & Willmann 1990). Actually they possess a hindwing trait that should be considered an autapomorphy of the Mecopterida (Kristensen 1975: 31): veins CuP and 1A are fused for some distance beyond the very base of the wing (Fig. 5; cf. Kristensen 1989: fig. 8). This apomorphy is clearly present in many extinct (e.g. Fig. 2) and extant taxa (Fig. 1; Tillyard 1919a: text-figs 3–4; etc.) but belongs neither to the ground plan of the Hymenoptera (Kukalová-Peck & Lawrence 2004: figs 3-4) nor to that of the Neuropterida + Coleoptera (ibid.: figs 5–8). Two other apomorphies visible in certain Protomeropidae lead us to place these insects in the Mecoptera, near – or perhaps within – the Pistillifera, a suborder defined by Willmann (1987) which turns out to be monophyletic provided that we rid it of the Boreidae (see e.g. Grimaldi & Engel 2005: fig. 12.1 where apomorphy 24 (sperm pump; right-hand clade) defines the Pistillifera *s. str.*, i.e. as conceived in the present paper).

The first of these apomorphies corresponds to the presence of Carpenter's organs (Figs 3–5) in the male hindwing (Novokshonov 1997, 2004). It occurs only in a fossil group (here informally called 'CO') that includes at least the Protomeropidae (Fig. 5; Novokshonov 2004: fig. 5e), Kaltanidae (notably *Altajopanorpa* Martynova 1948, see Fig. 4), and Permochoristidae, (*Agetopanorpa* Carpenter 1930, see Fig. 3); *Archepetromantis* Novokshonov 1995 (Novokshonov 1997: fig. 19); *Petromantis* Handlirsch 1904 (Aristov & Bashkuev 2008)).

The second apomorphy can be formulated like this: in the forewing, vein M4 conspicuously divided, i.e. bifid (Figs 1–2) or with several branches (Fig. 6). It is absent from the mecopteran ground plan (cf. Nannochoristidae) and is only rarely observed in non-mecopterans (never found in Diptera and Amphiesmenoptera). It occurs in the Meropeidae (Tillyard 1935; Byers 1991), the Eomeropidae (= Notiothaumidae) (Carpenter 1972; Novokshonov 1997), most Choristidae (Fig. 1), certain fossil Bittacidae (notably *Probittacus* Martynov 1927), a few Panorpidae (owing to intraspecific variability in *Panorpa* L. 1758, Willmann 1989: fig. 107) and several fossil groups, in particular the Permochoristidae (= Mesochoristidae, = Agetopanorpidae, = Eosetidae) and 'Orthophlebiidae' (Tillyard 1935; Rohdendorf ed. 1962; Willmann 1989). Actually the apomorphy 'forewing M4 divided' may characterize the Pistillifera *sensu lato*, i.e. Pistillifera *s. str.* (with secondary loss in many extant taxa) and a number of fossils (notably group 'CO', see Figs 2, 6; with secondary loss in e.g. certain Kaltanidae: Fig. 4), which may, or may not, belong to the Pistillifera *sensu stricto* (presence of sperm pump unverifiable). On account of this apomorphy, group 'CO' should be more closely related to Pistillifera *sensu stricto* than to Nannomecoptera (Nannochoristidae).

8. The Permotrichoptera: a group deserving ordinal status

Unlike the Protomeropidae (Novokshonov 1997; Rasnitsyn & Quicke eds 2002), the Microptysmatidae (= Uraloptysmatidae) (Novokshonov 1993b) possess medial spurs to, at least, the metathoracic tibiae (Ivanov 2002; Rasnitsyn & Quicke eds 2002: fig. 280c), a trait apparently incompatible with a placement in the Antliophora (see above: section 4). They may also differ from the Antliophora in keeping a bifid CuA (Figs 7, 8), a plesiomorphic trait in all probability (unlike the secondarily bifid CuA found in a few Mecoptera (cf. section 1.2): mainly Kaltanidae and Protomeropidae, i.e. close relatives of the Permochoristidae whose CuA is invariably simple). On the other hand, the Microptysmatidae cannot be ascribed to the Amphiesmenoptera since their ground plan lacks a characteristic 'double-Y' anal loop (see section 1.2), and seemingly retains nygmata between Rs and M (Fig. 8 – see section 2). Moreover they differ from Trichoptera and Lepidoptera in their forewing, which sometimes possesses fairly numerous subcostal crossveins, and in their hindwing whose veins M3 and M4 are never entirely merged together (Fig. 8). Accordingly we propose to place this family in its own order, namely the Permotrichoptera Martynova 1958 (**new status** – the group was originally conceived as a trichopteran suborder (Martynova 1958: 92)). The monophyly of the Permotrichoptera is supported by the distinctive forewing venation which characterizes the Microptysmatidae (Martynova 1958; Sukatsheva 1976; Kukalová-Peck & Willmann 1990; Novokshonov 1993b, 1997; Rasnitsyn & Quicke eds 2002): in particular, veins Rs1, Rs2 and M1 are divided (apomorphies) whereas vein M4 is always simple (plesiomorphy). This order belongs to the Mecopterida, as shown by the subbasal anastomosis of veins CuP and 1A in the hindwing (Fig. 8; Novokshonov 1993a: fig. 2b).

Conclusion

The sister-group relationship between fleas (Siphonaptera) and Boreidae seems rather well established (Kristensen 1999; Whiting 2002; Grimaldi & Engel 2005; etc. – but see also Beutel *et al.* 2009) and, among Recent Mecopterida, at least certain molecular studies (e.g. Whiting 2002) provide evidence that a monophylum gathers this lineage (Boreidae + fleas), the Nannochoristidae and the Pistillifera (excl. Boreidae; i.e. Hünefeld's and Beutel's (2005) concept of the Pistillifera Willmann 1987). Keeping the name Mecoptera and the ordinal rank for this monophylum is certainly recommendable (Kristensen 1999: fig. 9), even though – to date – only few morphological apomorphies turn out to support the monophyly of this order. Among these, one can now mention, tentatively, the 'pectinate' structure of the pretarsal claws (see section 5). We thus propose to treat as mecopteran suborders the four 'orders' recently considered by Whiting (2004: fig. 21.7), viz.: Nannomecoptera (Nannochoristidae only), Neomecoptera (Boreidae), Siphonaptera, and Pistillifera (a suborder corresponding to Whiting's 'Mecoptera' and defined by a distinctive type of sperm pump: Hünefeld & Beutel 2005).

A group of fossil insects (group 'CO', basically provided with Carpenter's organs: see section 7) can be placed in the order Mecoptera insofar as its forewing ground plan possesses, like that of the Pistillifera, a distinctly divided vein M4 (synapomorphy). Carpenter's organs (a male secondary sexual character) or a divided M4 in the forewing are apomorphies that may help to assign fossil wings to the Mecoptera. As redefined here, the order Mecoptera apparently dates back to the Upper Carboniferous (Nel *et al.* 2007), while the oldest known Amphiesmenoptera and Permotrichoptera (Microptysmatidae) are, respectively, from the Upper and Lower Permian. The Mecoptera would thus be much older than suggested by recently published molecular-clock analyses (Wiegmann *et al.* 2009a, b), which also propose a too recent origin for the order Coleoptera (Middle Permian whereas the earliest genuine Coleoptera have been recorded from the Lower Permian).

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