

The First Mecopteroids (Insecta: Papilionidea = Mecopteroidea) and the Origin of Scorpionflies (Panorpida = Mecoptera), with Description of a Legless Eruciform Larva from the Lower Permian of Tshekarda

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Abstract—The origin of insects of the mecopteroid complex and the early evolution of true scorpionflies are discussed. A legless eruciform larva, *Curvilarva tshekardensis* sp. nov., is described from the Lower Permian of Tshekarda.

INTRODUCTION

Among modern fauna, the superorder Papilionidea represents one of the largest groups of holometabolous insects, being slightly exceeded in terms of number of species only by beetles and hymenopterans. The earliest mecopteroids are known from the Early Permian and are represented by Trichoptera and Panorpida (= Mecoptera) (Tillyard, 1926; Martynov, 1940; Sukatcheva, 1976; Kukalová-Peck and Willmann, 1990). The rest of the mecopteroid orders have not been recorded from the Paleozoic, except for presumed and highly questionable remains of Diptera that have been found in the Permian continental deposits of France (Nel *et al.*, 1997). Moreover, one should remember that the placement of fleas in Papilionidea may be incorrect, since the males of all the rare Mesozoic insects that are believed to be related to fleas (Riek, 1970; Ponomarenko, 1976; Rasnitsyn, 1992) possess a well-developed aedeagus, and one clearly shows free volsellae. If the latter condition is not secondary, then fleas could represent a sister-group to mecopteroids and descend separately from some group ancestral to both (Rasnitsyn, 1992). We still know very little about the origins of mecopteroids, and, unfortunately, paleontological data do not throw much light on this problem.

With some justification, the extinct order Palaeomanteida (= Miomoptera), is considered the common ancestor of all holometabolous insects (Rasnitsyn, 1980a; Ponomarenko, 1983). However, one cannot exclude that holometabolans originated from some unknown ancestors they had in common with miomopterans (Fig. 1) rather than directly from the latter group, because none of the miomopteran groups possess a set of characters that would allow holometabolans to be derived from it without a great deal of interpolation (Novokshonov and Zhuzhgora, 2004).

SEPARATION OF MECOPTEROIDS

The first mecopteroids are close to neuropteroids (Myrmeleontidea = Neuropteroidea) and originate from primitive members of the latter superorder (Martynova, 1957; Rasnitsyn, 1980b) the larvae of which had not yet become specialized in predatory feeding. The earliest neuropteroids entered the fossil record simultaneously with mecopteroids.

We will compare only those characters of the first mecopteroids and neuropteroids that are visible in the Permian fossils.

True neuropterans appear to be most similar to the earliest mecopteroids in wing structure. All other members of this superorder show specialized venation and cannot be considered relatives of the oldest mecopteroids, even if they enter the fossil record at the same time as the first scorpionflies (Novokshonov, 1997).

Thus, Jurinida (= Glosselytrodea) are easily derivable from neuropterans and show no synapomorphies with scorpionflies (Novokshonov, 1998a).

Paleozoic Corydalida (= Megaloptera), known from the single Permian family Parasialidae Ponom., possess impoverished venation, forewings with MP+CuA anastomosis, hindwings an enlarged anal area (tucked under the wing in repose), and a lost CuA fork (Ponomarenko, 1977; Novokshonov, 1993). None of these characters are by any means representative of the first mecopteroids.

Permosialidae were long considered a Paleozoic group of megalopterans, but Riek (1976) and Rasnitsyn (1977) have shown that they belong to Palaeomanteida. Despite the fact that they possess the most archaic venation among all miomopterans (Novokshonov, 1997), they cannot be ancestral to mecopteroids, because the members of the genus *Permosialis* Mart. have a shortened and three-segmented tarsus (Novokshonov and Rasnitsyn, 2001), whereas the genus *Permonka* Riek appeared very late, at the end of the Per-

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mian, and already had wings that were folded flat in repose (Rasnitsyn, 1980a).

The Permian family Letopalopteridae O. Mart., formerly assigned to Raphidiida (Martynova, 1961; Ponomarenko, 1980), has recently been transferred to the order Hypoperlida. This family was established for distinctive insects from the Upper Permian of Arkhangel'sk region and assigned to snakeflies because of their body structure, above all because of their long pronotum and long ovipositor. However, reexamination of the material revealed that the hind tarsus was mistaken as the ovipositor (Novokshonov, 1998b; Novokshonov and Willmann, 2002) (Figs. 2a, 2b). Moreover, the pronotum is still only slightly elongate in the more primitive Early Permian letopalopterids (Novokshonov, 1998b) (Fig. 2c) and comparatively long in some typical hypoperlids, such as *Tshekardobia osmylina* A. Rasn. An undescribed "snakefly" specimen from the Arkhangel'sk region, mentioned by Ponomarenko (1980), belongs to an unknown species of Letopalopteridae. The second Permian family of "snakeflies," Sojanoraphidiidae O. Mart., which does indeed possess a long, slender ovipositor (Fig. 2d), was later transferred to the order Grylloblattida (Storozhenko and Novokshonov, 1995). This assignment was further confirmed when another genus of Sojanoraphidiidae possessing the same long and slender ovipositor along with typical grylloblattid venation was discovered in Tshekarda (Novokshonov and Storozhenko, 1996) (Fig. 2e). Thus, according to present views, none of the members of the order Raphidiida occurred in the Paleozoic.

It remains to compare mecopteroids with true neuropterans, a comparison that seems simple only at first sight. The point is that, in the Early and Late Permian, a variety of archaic forms existed that obviously belonged to the primitive scorpionflies, caddisflies, or neuropterans, but that they should be allocated to any of these three groups is virtually unprovable.

Thus, many forewings of Neuroptera, from various Permian localities, exhibit a primitive rudimentary anal loop (Novokshonov, 1996) characteristic of caddisflies (*Permithonopsis ivensis* Mart., *Permosisyra pauvovenosa* (O. Mart.), *Eopsychops angaridensis* O. Mart., *Sauropsychops kazakhstanensis* Vilesov et Novoksh.) (Figs. 3a–3c; Pl. 12, fig. 1). This structure is common in several insect groups (Grodnitsky, 1995); however, in this case, the loop possibly provided for a more secure fixation of wings when in repose. In the living caddisflies, at least, the main point of fixture is between the overlapping posterobasal areas of the forewings.

On the other hand, the most primitive mecopteroid insects from the Artinskian of the Czech Republic have either an underdeveloped anal loop or none at all (Figs. 3g–3i) (Kukalová-Peck and Willmann, 1990); however, their closest relationship to the true caddisflies, Protomeropidae Till., from the same or nearly synchronous deposits is beyond doubt (Figs. 3d–3f). I have recently found a similar wing with an underde-

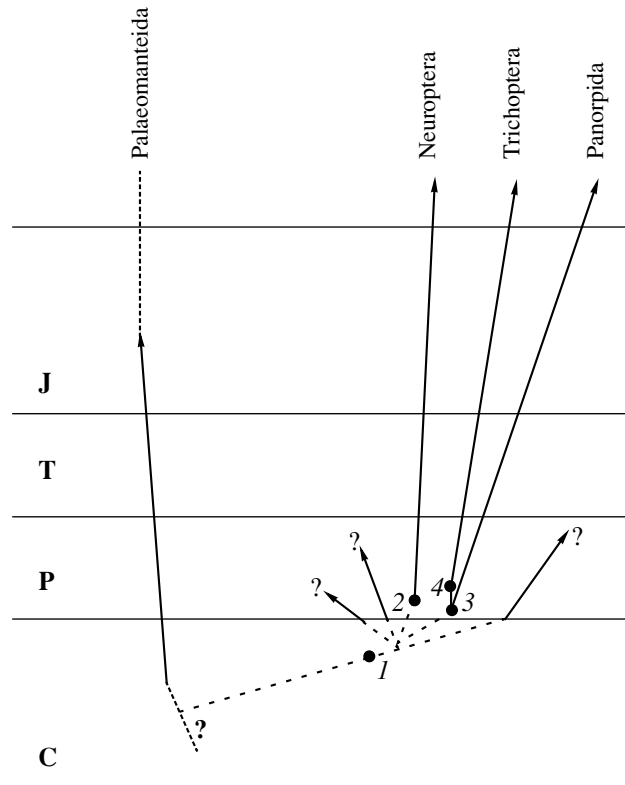


Fig. 1. Scheme of the phylogenetic relationships between the orders Palaeomanteida, Neuroptera, Trichoptera, and Panorpidia. Unknown or still unrecognized Carboniferous insects or Permian insects of uncertain systematic position are marked with a "?" sign. Synapomorphies: (1) MA transferred onto RS, MA base still long and oblique; possibly, considerable reduction of external ovipositor; (2) partial polymerization of RS+MA without active participation of MA, crowding of SC branches near the wing apex, development of trichosors, enlargement of the hindwing anal area with part of the anal veins being tucked under when in repose; (3) partial polymerization of RS+MA with active participation of MA, MA base transformed into short crossvein, in male hindwings Carpenter's organs developed on SC branches, in hindwings of both sexes CuP and A₁ partly fused; and (4) anal loop formed in forewings.

veloped anal loop in Tshekarda (Perm region; Kun-gurian) and provisionally identified it as *Marimerobius* sp. This specimen clearly shows that the apices of A₃ and A₂ do not form the regular loop characteristic of the other protomeropid caddisflies (Pl. 12, Fig. 2).

Moreover, many other Lower and Upper Permian localities contain forms that can be reliably assigned neither to scorpionflies, nor to caddisflies, nor to neuropterans. These are *Moravochorista carolina* Kukalová-Peck et Willmann from the Czech Republic (Fig. 4a), *Persona incognita* Novoksh. and *Tshekarchiereus rasnitsyni* Novoksh. from Tshekarda (Figs. 4b–4d), *Karaungira shcherbakovi* Novoksh. et Sukatch. from the Late Permian of Karaungir (Kazakhstan) (Fig. 4e), and *Anormochorista oligoclada* Till.

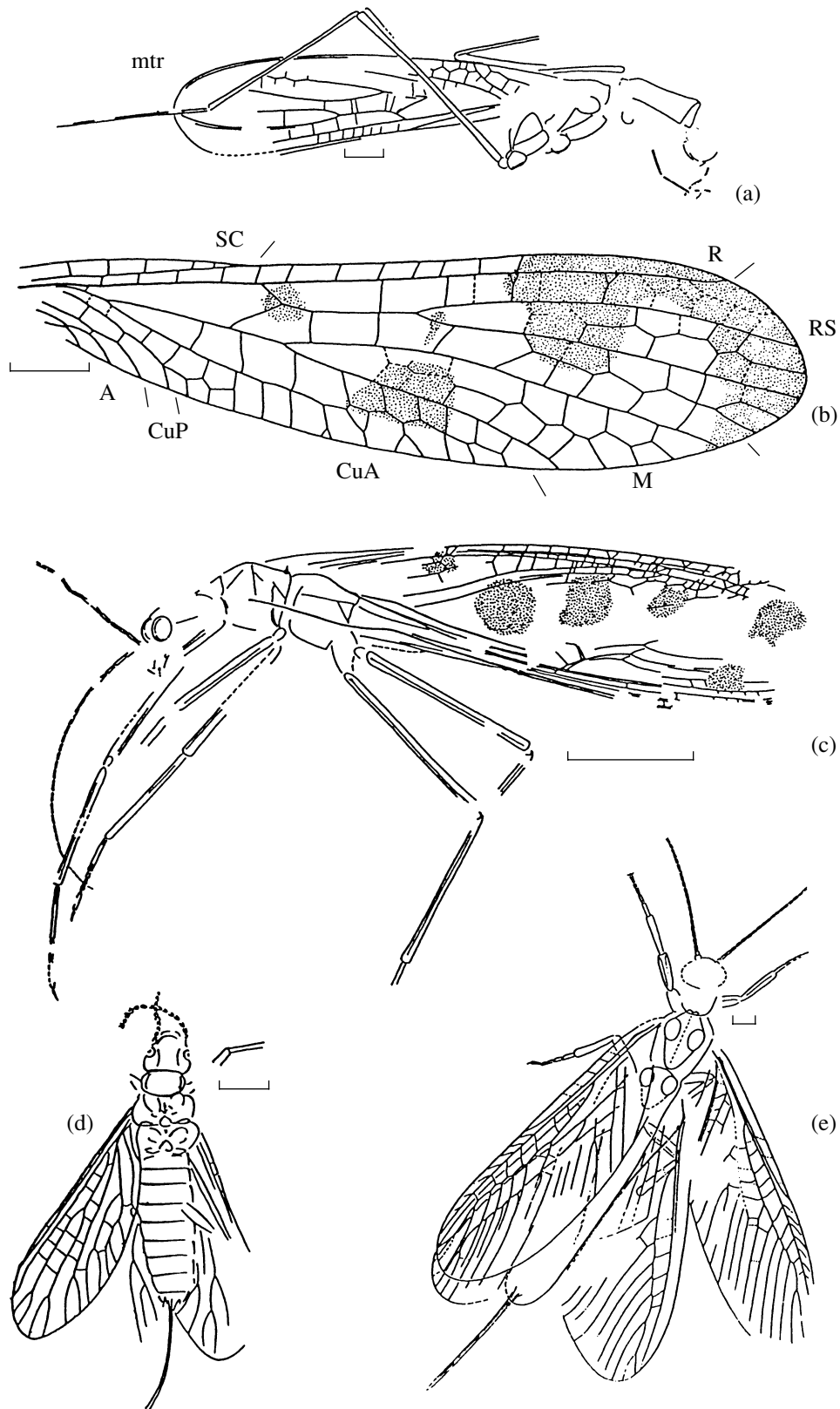


Fig. 2. Permian insects formerly erroneously assigned to Raphidiida: (a) and (b) members of the genus *Letopaloptera* O. Mart. (Hypoperlida) (from Novokshonov and Willmann, 2002), (c) member of the genus *Permindigena* Novoksh. (Hypoperlida) (from Novokshonov, 1998b), (d) member of the genus *Sojanoraphidia* O. Mart. (Grylloblattida) (from Ponomarenko, 1980), (e) member of the genus *Aibolitus* Novoksh. et Storozh. (Grylloblattida) (from Novokshonov and Storozhenko, 1996). Abbreviations: (mtr) hind tarsus; vein symbols standard. Scale bar in Figs. 2a, 2b, and 2e, 1 mm; in Fig. 2c, 5 mm; in Fig. 2d, 3 mm.

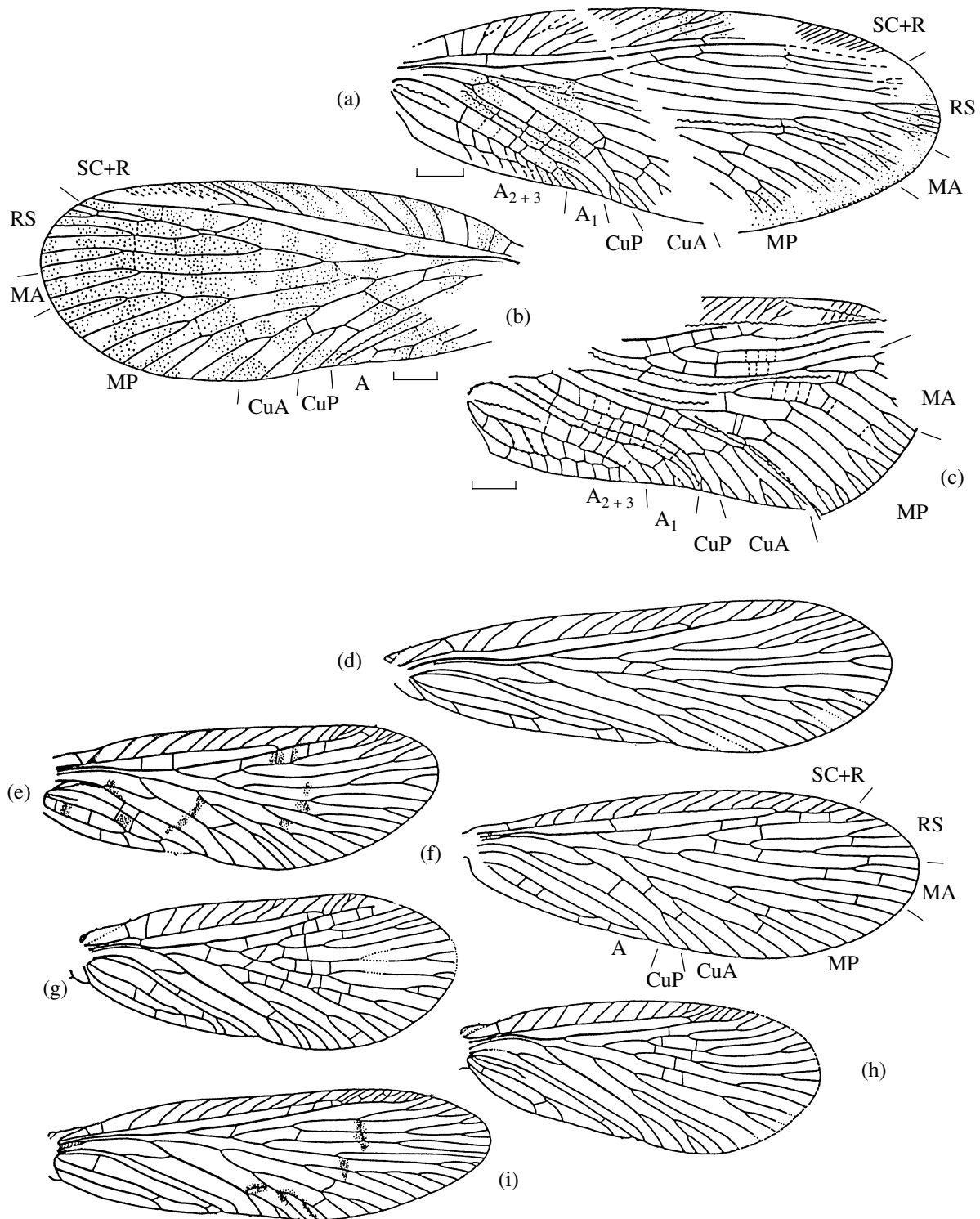


Fig. 3. Forewings of Permian Neuroptera Permithonidae (a)–(c) and Trichoptera Protomeropidae (d)–(i): (a) *Permithonopsis ivensis* Mart., (b) *Permosisyra paurovenosa* (O. Mart.), (c) *Eopsyrops angaridensis* O. Mart., (d) *Stenomerope spinari* Kukal.-P. et Willm., (e) *Pseudomerope mareki* Kukal.-P. et Willm., (f) *Platychorista venosa* Till., (g) *Pseudomerope oborana* Kukal.-P. et Willm., (h) *P. oborana* (paratype), and (i) *Stenomerope spinari* (paratype). Vein symbols standard. Figs. 3a–3c from Novokshonov, 1996, Figs. 3d–3i from Carpenter, 1930 and Kukulová-Peck et Willmann, 1990. Scale bar 1 mm in Figs. 3a–3c, other figures not to scale.