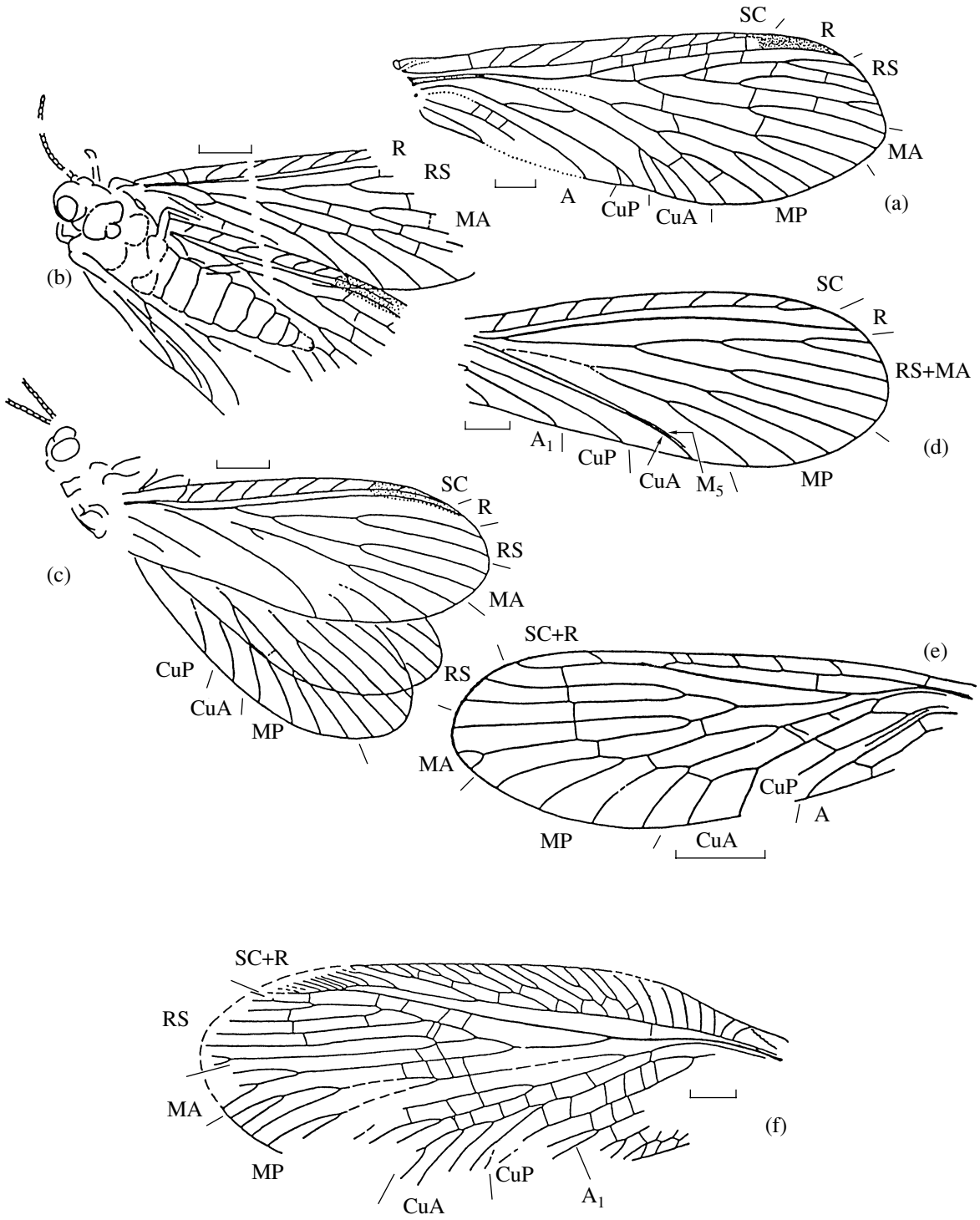

Fig. 4. Permian insects probably belonging to (a)–(e) mecopteroids or neuropteroids and (f) Permian Neuroptera: (a) *Moravochorista carolina* Kukal.-P. et Willm. (Kaltanidae?) (from Kukalová-Peck et Willmann, 1990), (b) and (c) *Persona incognita* Novoksh.(Personidae) (from Novokshonov, 1995), (d) *Tshekarchiereus rasnitsyni* Novoksh.(Tshekarchiereidae) (from Novokshonov, 1997), (e) *Karaungira shcherbakovi* Novoksh. et. Sukatch.(Karaungiridae) (from Novokshonov and Sukatcheva, 1993), and (f) forewing of *Permerobius latibasis* (O. Mart.) (Permithonidae) (from Novokshonov, 1996).

from the Lower Permian of North America. Thus, these species have been assigned to separate families.

These facts support the idea that, at the end of the Carboniferous and at the beginning of the Permian, a large insect group (archaic diversity) existed that may have had a common ancestry with miomopterans and gave rise to both Papilionidea and Myrmeleontidea.

An MA branching pattern, in which RS+MA appears dichotomous rather than pectinate, was cited as one of the most important wing characters distinguishing mecopteroids from neuropteroids (Rasnitsyn, 1980b). However, Permian neuropterans often show deviations from the strictly pectinate pattern of RS+MA, with aberrant forks appearing on its branches here and there (Ponomarenko, 1980; Vilesov and Novokshonov, 1994; Novokshonov, 1996) (Fig. 4f). The complete reduction of the base of MA (which shifted onto RS) has been hypothesized as another character for mecopteroids (Rasnitsyn, 1980b). It has been established, however, that the MA base was retained in the hindwings of the earliest Papilionidea as a short r-m crossvein (Novokshonov, 1992) (Figs. 5a–5c).

We can now list the main characters shared by the Permian mecopteroids and neuropterans: a slender body; moderately long legs with five-segmented tarsi; elongate conical coxae, inclined caudally; a somewhat inclined pleural region; unmodified mouthparts; a comparatively short pronotum; short, presumably three-segmented cerci (unknown for neuropterans); an external ovipositor apparently much reduced; RS pectinate, but already incorporating MA; in the forewings, CuA with a simple fork, anal loop absent; in the hindwings, the MA base either long and curved or short; the anal area of the hindwing slightly enlarged, without some anal veins being tucked under in repose; CuA concave; the M5 base short and oblique; and CuP and A_1 free.

Mecopteroids underwent a partial polymerization of RS+MA, with MA becoming repeatedly dichotomously branched; in their hindwings, CuP and A_1 became partly fused, and (in males) the Carpenter's organs were developed at the SC branches (Figs. 5b–5e). The main "acquisitions" of neuropterans have been discussed in detail in another paper (Novokshonov, 1997).

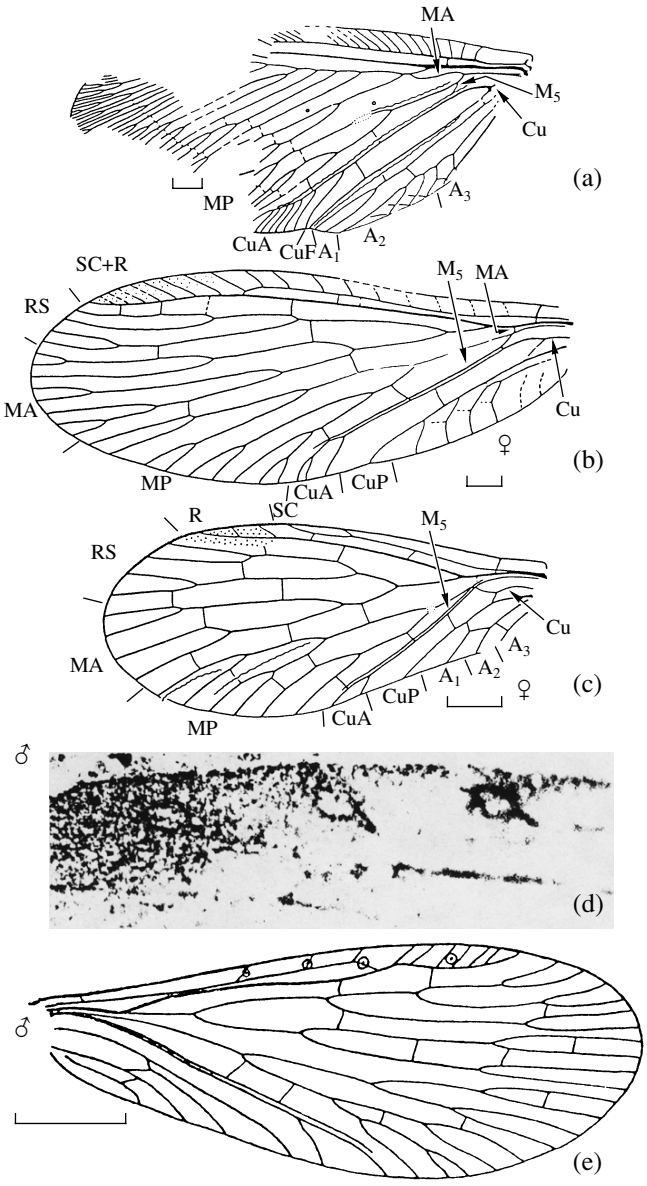

Fig. 5. Hindwings of (a) Neuroptera (b)–(e) mecopteroids: (a) *Permopsychops saurensis* Novoksh. et Vilesov (Permithonidae), (b) *Marimerobius* sp., female (Protomeropidae), (c) and (d) *Altajopanorpa* sp. (Kaltanidae): (c) female, (d) Carpenter's organs of male (Figs. 5a–5d from Novokshonov, 1997), (e) *Platychorista venosa* Till. with Carpenter's organs (Protomeropidae) (after Carpenter, 1930).

THE FIRST SCORPIONFLIES

The most primitive, ancestral order of Papilionidea is Panorpida. But what group of fossil mecopteroids should be regarded as representing the first scorpionflies? Apparently, we need not consider here in detail the hypothetical reconstruction of the wings of the first scorpionflies that was proposed by Tillyard (1919) and was based on finds of Orthophlebiidae Handl.—which were numerous in that time, whereas other fossil representatives of the order remained virtually unknown (Fig. 6a). Nowadays, the problem of the scorpionfly groundplan widely depends on the solution of the problem of the Permian family Kaltanidae O. Mart. (Fig. 6b). The comparatively ancient age and primarily polymerized venation of kaltanids make their being the most primitive scorpionflies almost obvious. The history of this problem has been treated in detail in another paper (Novokshonov, 1998c); thus, it is here necessary to consider a completely different problem connected with kaltanids.

The point is that the family Kaltanidae appears in the fossil record quite late, only in the Late Permian, whereas representatives of their presumed and most

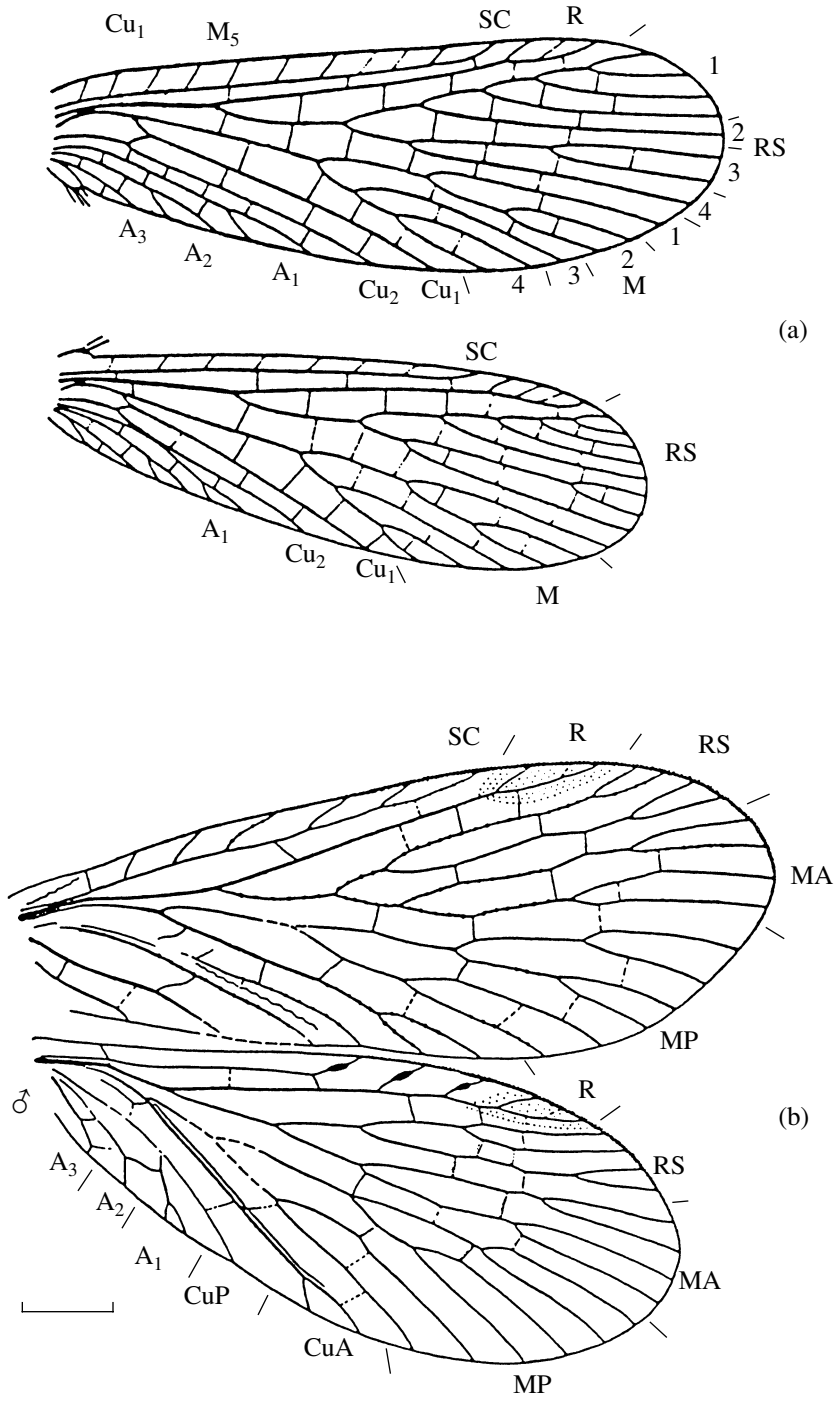

Fig. 6. Fore- and hindwings of the first scorpionflies (hypothetical and fossil): (a) hypothetical reconstruction of the first scorpionfly after Tillyard (1919; from Willmann, 1989; vein symbols by Tillyard), (b) *Altajopanorpa pilosa* (O. Mart.) (from Novokshonov, 1997).

probable descendants, scorpionflies of the family Permochoristidae, were already common and numerous in two Early Permian localities (Tshekarda in the Urals and Elmo in Kansas; in other Early Permian localities, scorpionflies have not yet been recorded).

However, if you refer to a map of climatic zones for Early Permian landmasses (Chumakov and Zharkov, 2002), you will notice that both localities with the Early Permian Permochoristidae scorpionflies fall within semiarid and arid climatic zones, whereas all future