

Fig. 4. Miomopterans of the family Palaeomantiscidae: (a) habitus of female of *Sellardsiopsis conspicua* G. Zal.; (b) habitus of female of *Palaeomantina pentamera* A. Rasn. (after Rasnitsyn, 1977); (c) fore- and hindwings of one specimen of *P. pentamera* (specimen PGU, no. 2/307); (d) forewing base of the same specimen (the white arrow points to the junction of A1 and A2). Scale bar for Fig. 4c, 1 mm; other figures are out of scale.

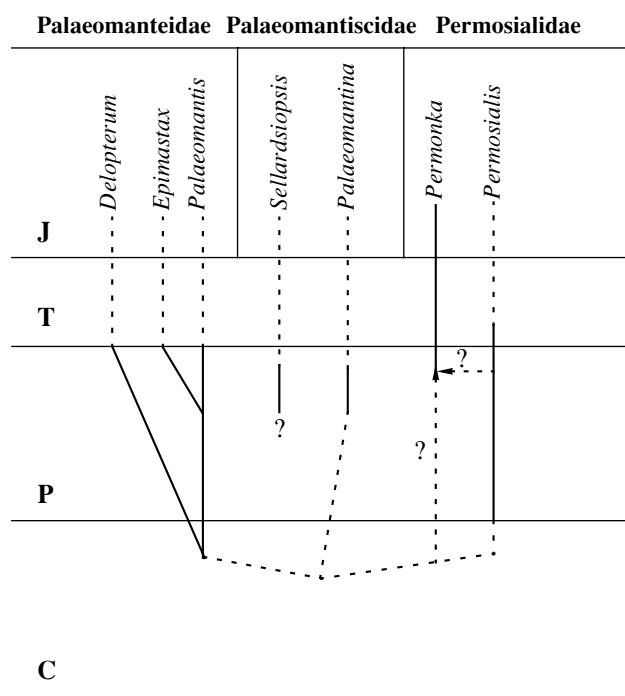


Fig. 5. Preliminary scheme of phylogenetic relationships within Palaeomanteida.

PHYLOGENY OF PALAEOMANTEIDA

Notwithstanding the fact that the number of known miomopteran families and genera is small, their internal phylogenetic relationships are poorly understood. None of the miomopteran families can be derived from any other such families: the oldest family, Palaeomanteidae, which retains the longest cerci in the order (genus *Palaeomantis*; presumed plesiomorphy), cannot be ancestral to the remaining miomopterans, as its members have a four-segmented tarsus (five-segmented in *Palaeomantina*) and CuA anastomosing with M in the forewings (free in Permosialidae). However, the genus *Sellardsiopsis* may be derived from Palaeomanteidae. Within the family Palaeomanteidae, the genus *Epimastax* is easily derivable from *Palaeomantis*: the Tshekarda locality has yielded a hindwing of *Palaeomantis tshekardensis* Novoksh. that combines the characters of both genera. Owing to the deep CuA fork and wide area between CuA and CuP, this wing appears to be more advanced compared to the common representatives of *Palaeomantis* and similar to the Upper Permian genus *Epimastax*, the latter being distinct only in the greater multibranching of RS (Novokshonov, 2000). The reduced venation pattern of *Delopterum* is likewise derivable from that of *Palaeomantis*.

Palaeomantiscidae appear late in the fossil record, synchronous with Permosialidae. The genus *Sellardsiopsis* has a four-segmented tarsus and jumping hind legs unique among genera of the order. Although the genus *Palaeomantina* has a five-segmented tarsus, it is

apomorphic in having elongate mandibles and in several of its wing characters (see above). One cannot exclude the possibility that the genus *Sellardsiopsis* originated from an immediate ancestor of *Palaeomantina* with a more archaic wing structure.

Permosialidae, which retain a primitive relationship between M and CuA in the forewings, likewise cannot be ancestral to other miomopterans, because they appeared quite late, only in the Early Permian. Moreover, the genus *Permosialis* has shortened tarsi (apparently of only three segments). The genus *Permonka* appeared even later (Late Permian of South Africa) and has flat (i.e., more compact than in other miomopterans) wing folding. A reversal from flat to less perfect rooflike wing folding is hardly probable (Rasnitsyn, 1980a). The origin of this genus is unclear, all the more so as it appeared very late, and information on its body structure is insufficient. One can assume that it is related to *Permosialis* (CuA in forewings not anastomosing with M) and originated either directly from it (then, shortened three-segmented tarsi may be expected in *Permonka*) or from a more primitive, still unknown miomopteran group that retained free CuA and M.

It is difficult to expect that any future finds will considerably elucidate the origin and phylogenetic relationships within the order Palaeomanteida, unless additional data on the composition and morphology of miomopterans from the Middle Carboniferous of the Mazon Creek locality appear. Until today, there has been only one specimen known from that site, and this specimen is best suited to the diagnosis of the family Palaeomanteidae (Rasnitsyn, 2002, p. 168, text-fig. 214). The greater part of the materials from the richest miomopteran locality, Tshekarda, has been studied in considerable detail: all three families were found there, and the structure of their bodies and wings was examined. However, these results have complicated rather than alleviated this problem. It turns out that none of the known taxa possess the full set of plesiomorphies, such as the rooflike wing folding, multibranching SC terminating on the anterior wing margin, free M_5 base and an absence of anal loop in the forewing, concave CuA in the hindwing, unmodified femora, and five-segmented tarsi.

For similar reasons, it is difficult to determine which of the miomopteran groups is most closely related to the earliest hymenopterans and mecopteroids. According to Ponomarenko (1980), the known miomopterans seem to contain no forms ancestral to neuropteroids.

Does the above statement mean that the order Palaeomanteida should be excluded from the supposed ancestors of Holometabola? Most probably no. Despite the fact that every miomopteran group has proven to be heterobathmous, the order as a whole exhibits the same set of characters that is characteristic of the earliest hymenopterans, mecopteroids, and neuropteroids (Novokshonov and Zhuzhgova, 2001).

In other words, the question is whether or not reconstruction of the ancestors of Holometabola on the basis

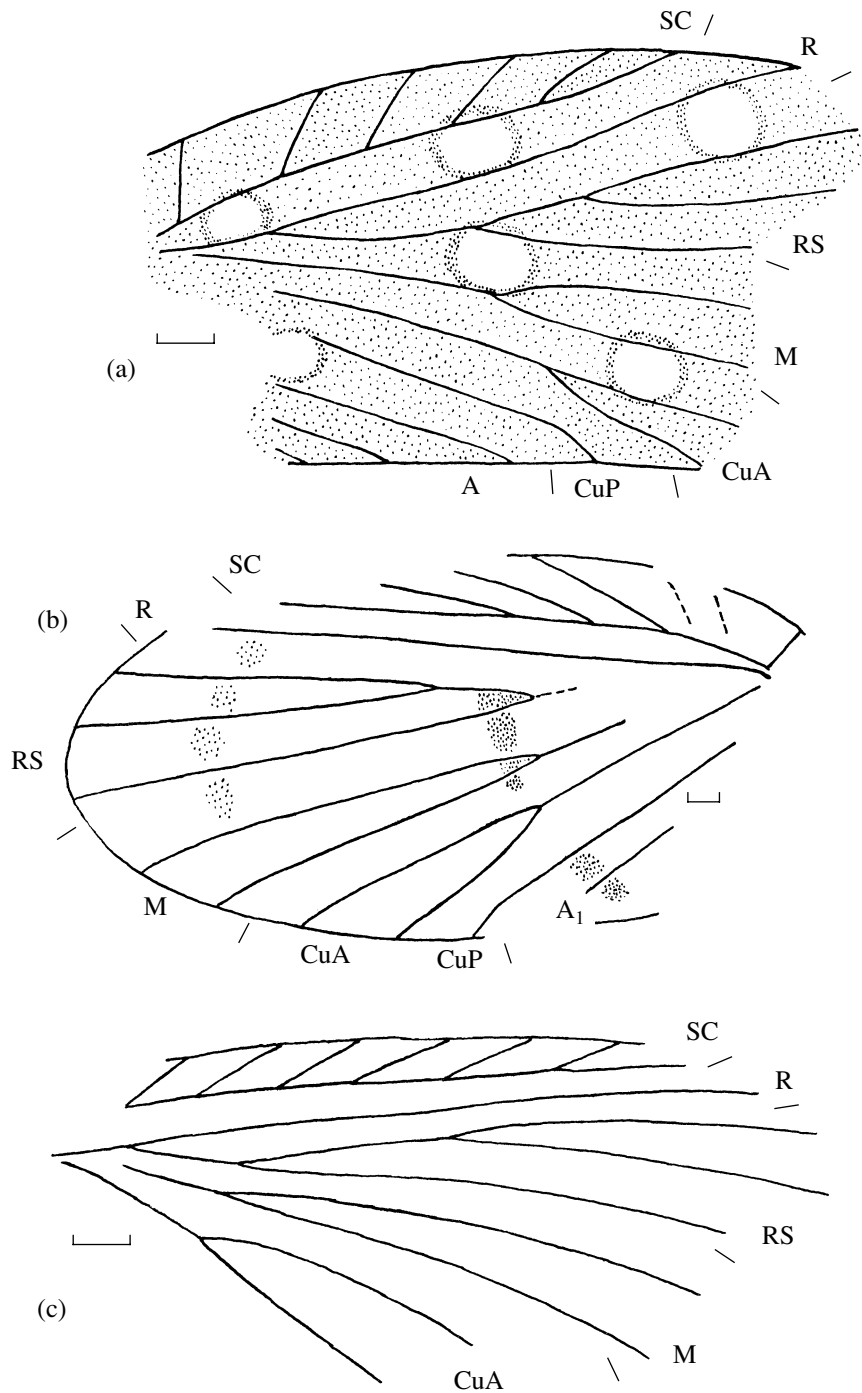


Fig. 6. New species of *Permosialis*: (a) and (b) *P. ualentovae* sp. nov., (a) holotype PIN, no. 1366/349, male?, (b) paratype PIN, no. 1366/379, female?; (c) *P. triassica* sp. nov., holotype PIN, no. 2555/2066. Scale bar 1 mm.

of our knowledge of miomopterans will yield a character set that fits the diagnosis of Palaeomanteida. Probably yes, even if no possible ancestors have been yet found among them.

Based on all available data, a preliminary phylogenetic tree is constructed to show the possible evolutionary interrelations within the order (Fig. 5; argumentation see above).