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Discussion of the System and Phylogeny of the Order Palaeomanteida (= Miomoptera) with Description of New Representatives of the Genus *Permosialis* Mart. from the Late Permian of Kirov Region and Triassic of Kyrgyzstan

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Abstract—Taxonomic and phylogenetic relationships within the order Palaeomanteida are discussed. Morphological characteristics of little-known miomopteran taxa are supplemented. An idea of sexual dimorphism in the species of *Permosialis* Mart. is advanced. *Permosialis ualentovae* sp. nov. from the Late Permian of the Kirov region and *Permosialis triassica* sp. nov. from the Triassic of Kyrgyzstan are described.

INTRODUCTION

The order Palaeomanteida (= Miomoptera), which occurred from the Middle Carboniferous to the Early–Middle Jurassic, is considered to be a common ancestor of all holometabolous insects (Rasnitsyn, 1980a). This order was transferred into Scarabaeiformes (= Holometabola) from Gryllones (= Polyneoptera) by Rohdendorf (1977), but without any comment (Rasnitsyn, 1980a). Rasnitsyn (1980a) analyzed the problem in detail and noted that the nymphs described as being miomopteran (Sharov, 1957) most probably belong to Gryllones and that the segmented cerci of Palaeomanteida do not preclude assigning them to holometabolans, because three-segmented cerci are retained in living scorpionflies and, therefore, should also be present in primitive Scarabaeiformes. In addition, Rasnitsyn (1980a) listed those features of Palaeomanteida that are characteristic of Scarabaeones (Palaeoptera, Para- and Oligoneoptera), but the full set of said features never occurs in Gryllones. These are wings that are folded rooflike over the abdomen in repose (except for *Permonka* Riek), a hindwing anal area not tucked under in repose, cryptosterny, the third valvulae of the ovipositor forming its sheath, and the male gonocoxae and gonostyles forming a clasping organ. One more character listed is generally specific for holometabolous insects: additional medial articulation of pterothoracic coxae. Therefore, in adult morphology, miomopterans turned out to be, on the one hand, sufficiently advanced to be included in Scarabaeiformes and, on the other hand, so primitive and ancient that they might be ancestral to the remaining Scarabaeiformes, all the more so as no other group is known to meet the required conditions. Since no smooth transition has been uncovered between Palaeomanteida and any other holometabolous insect order, they are considered to be a separate superorder. The adult morphology of miomopterans suggests that they lived in open rather than cryptozoic habitats and, probably, fed on gymnosperm strobili (Rasnitsyn, 1980a). For a long time, there was no direct evidence of such trophic relationships; they have been confirmed, however, by pollen found in the gut of miomopterans belonging to Palaeomantiscidae and Palaeomanteidae from the Lower Permian of Tshekarda (Rasnitsyn, pers. comm.; the authors' personal observations). Taking into account the morphology of the ovipositor in Palaeomanteida, it appears that their larvae fed on pollen in more or less ripe gymnosperm cones, moving between the scales from one microsporangium to another. Hymenopterans form a direct continuation of this lineage; another group of miomopteran descendants consists of beetles, neuropteroids, and mecopteroids (Rasnitsyn, 1980a). The beetles represent a separate lineage, which is related to almost equal extents to both mecopteroids and neuropteroids; the larvae of the first beetles were apparently xylomycetophagous; the neuropteran larvae were predatory, whereas the first mecopteroids probably became detritivorous with a tendency toward being necrozoophagous (Ponomarenko, 1983). None of the known Carboniferous groups of insects has been identified as ancestral to Palaeomanteida.

MATERIAL

Collections of the Paleontological Institute of Russian Academy of Sciences (PIN) and Perm State University (PGU) were studied. All specimens are stored at PIN.

SYSTEM OF THE ORDER

Data on the taxonomy of miomopterans have been summarized by many authors (Martynova, 1962; Riek,

†Deceased.

1976; Kukalová, 1963; Rasnitsyn, 1980a, 1980b; Carpenter, 1992; Storozhenko, Novokshonov, 1999; Novokshonov, 2000; Rasnitsyn, 2002). Currently, Palaeomanteida are thought to comprise the family Palaeomanteidae Handl., which includes *Palaeomantis* Handl. (Late Carboniferous–Permian of Eurasia), *Delopterum* Sell. (Late Carboniferous–Permian of Eurasia and North America) and *Epimastax* Mart. (Late Permian of eastern and northeastern Europe); Permosialidae Mart., which includes *Permosialis* Mart. (Permian–Triassic of Eurasia and Australia) and *Permonka* Riek (Late Permian–Early and Middle Jurassic of Eurasia and South Africa): and Palaeomantiscidae A. Rasn., which includes *Sellardsiopsis* G. Zal. (Early Permian of the Urals) and *Palaeomantina* A. Rasn. (Early Permian of the Urals). The reasons for the taxonomic changes and the status of those genera that were previously known but are not listed here have been discussed in detail by Rasnitsyn (2002).

Miomopterans from the Middle Carboniferous of the Mazon Creek locality have not yet been described (see below). Late Carboniferous miomopterans have been discovered in several localities within France, Germany, and the United States, where they are represented by two genera, *Delopterum* and *Palaeomantis* (Rasnitsyn, 2002). Thus, the earliest known miomopterans belong to the family Palaeomanteidae. This suggests that future studies of their morphology will apparently be most useful in resolving the problems of both the phylogeny of the order and the origin of Holometabola. The remaining miomopteran families appeared only in the Early Permian, virtually synchronously with the first scorpionflies, caddisflies, neuropterans, and beetles. Hymenopterans (order Vespida) are known only from the Triassic onward.

The family Palaeomanteidae comprises most of the representatives of the order and is characterized by the following main wing features: wing folded rooflike; forewings with a slightly thickened membrane, relatively narrow costal area, and with several anterior SC branches (up to seven in *Epimastax*) or, rarely, no SC branches (*Delopterum*); in forewings, M and CuA anastomose subbasally for a greater or lesser but still relatively long distance, i.e., the base of M_5 is absent as a separate vein. This last feature is supposedly a secondary development in Palaeomanteida, the original state having been a retention of the free M_5 base that was fused to CuA to form a Y-shaped figure, as in miomopterans Permosialidae and in all archaic mecopteroids and neuropterans (Novokshonov, 1997). It is interesting here to analyze the course of the corresponding veins in the forewing in the reconstruction of a hypothetical hymenopteran ancestor (Rasnitsyn, 1980a, text-fig. 37a; p. 36). The section labeled as M+CuA may be interpreted as the M base, whereas the short crossvein running down to CuP may be treated as the CuA base. Thus, M and CuA anastomose for a distance and, then, again diverge (Fig. 1a; the parenthesized vein designations are after Rasnitsyn), which is characteristic of most miomopterans (Palaeomanteidae and Palaeomantiscidae). If so, miomopterans of the family Permosialidae should, perhaps, be excluded from the supposed ancestors of hymenopterans and may only be considered to be ancestral to archaic mecopteroids and neuropteroids. On the basis of its morphology, the genus *Palaeomantis* (see below), which is apomorphous only in having four-segmented tarsi, could be nearest to the origin of hymenopterans.

In the Permian, *Palaeomantis* and *Delopterum* became especially diverse and widespread. Their morphology is quite well known today, mainly due to numerous finds in the Lower Permian of the Urals (Novokshonov, 2000). The representatives of *Palaeomantis* (body structure being known for *P. aestiva* Novokshonov, 2000) are medium-sized insects (Figs. 1b–1f). The antennae are setaceous and about as long as the forewing; the eyes are ovoid and weakly convex; the ocelli form a single group; the maxillary palps are long, and the labial palps are much shorter. The pronotum is large, rounded quadrangular, but slightly shorter than it is wide; the meso- and metanotum are subdivided as usual; the pleural region is of generalized structure. The tarsi are four-segmented. The male abdomen bears long, multisegmented cerci, forming a forceps-shaped figure (probably, in *P. aestiva*, cerci aided in fixing the female abdomen during copulation); the gonocoxae are large, apparently firmly fused to each other by their upper and lower processes; the gonostyles are small and curved; nearly all specimens show a central baculiform sclerotized process, the tip of which could extend far beyond the gonostyle apices (presumably, this is an evaginable penis); a similar structure of the male genitalia is characteristic of both some mecopteroids (caddisflies) and hymenopterans (Rasnitsyn, 1969, p. 138, text-figs. 244–250). The female abdomen bears a powerful, straight, and wide ovipositor reaching up to the apices of the folded wings; no armature is traceable on the outer valves, but often a narrow pair of the inner valves reaching the ovipositor tip is clearly visible due to their distinct transverse striations (very similar structures are present in the ovipositors of some extant hymenopterans: Rasnitsyn, 1969, p. 132, text-fig. 236). In the forewings, SC terminates slightly distal to the wing midlength, with four or five anterior branches; the costal area is about as wide as the subcostal one; R has a more or less distinct scooplike bend distally; RS has normally three or four terminations (even five in aberrant specimens); the basal portion of M is often desclerotized; the CuA fork is deep, sometimes longer than its stem; A1 is of usual structure; A2 and A3 sometimes form a peculiar cell near the wing base. The hindwings are similar to the forewings but differ from them in the same characters as in most other palaeomanteids. It is worth mentioning that an undescribed complete female specimen of *Palaeomantis* sp. (cited as ?Miomoptére in the original description) from the Upper Carboniferous of France is virtually indistinguishable, as judged from the figures

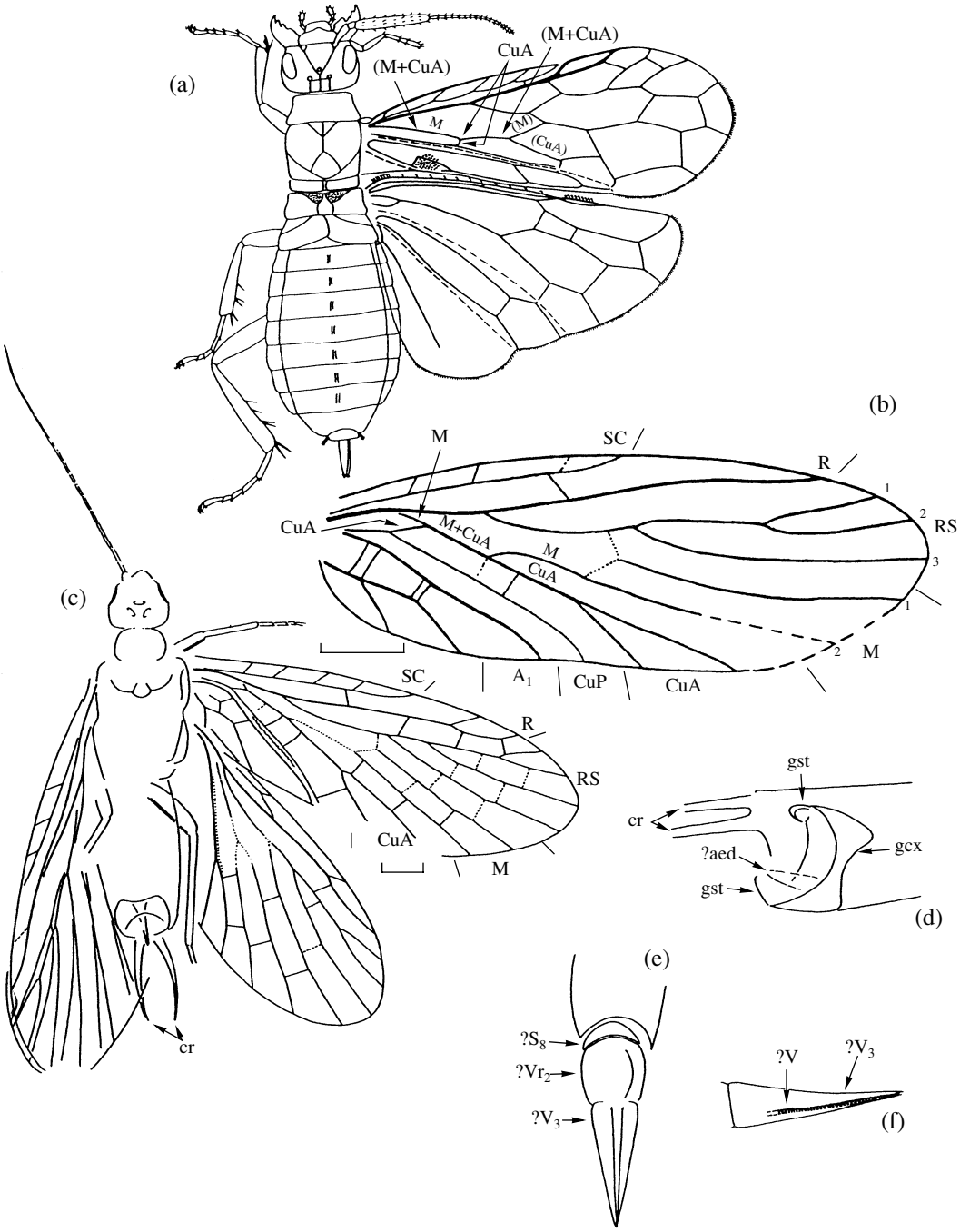

Fig. 1. Hymenopterans and miomopterans of the family Palaeomanteidae: (a) hypothetical hymenopteran ancestor (after Rasnitsyn, 1969, 1980a); (b) forewing of *Palaeomantis laeta* Novoksh. et Zhuzhg. (after Novokshonov and Zhuzhgova, 2002); (c–f) *Palaeomantis aestiva* Novoksh.: (c) habitus, (d) apex of male abdomen laterodorsally, (e) apex of female abdomen ventrally, (f) ovipositor laterally (after Novokshonov, 2000). Designations and abbreviations in Figs. 1–6 standard. Scale bar for Fig. 1b, 1 mm; other figures are out of scale.

(Oudard, 1980, p. 39, text-fig. 3; p. 47, text-fig. 19), from the Early Permian *Palaeomantis* from the Urals.

Representatives of the genus *Delopterum* (Figs. 2a–2c) are small palaeomanteids with long setaceous antennae, which are slightly longer than their forewings, and ovoid and weakly convex eyes. The pronotum is usually narrow; the meso- and metanotum are rounded triangular. The tarsi are four-segmented (in undescribed specimens from PIN and PGU). The abdomen does not even approach the apices of the folded wings in both sexes and is slenderer in males than in females. The gonocoxae are large; the gonostyles are long, slender, and

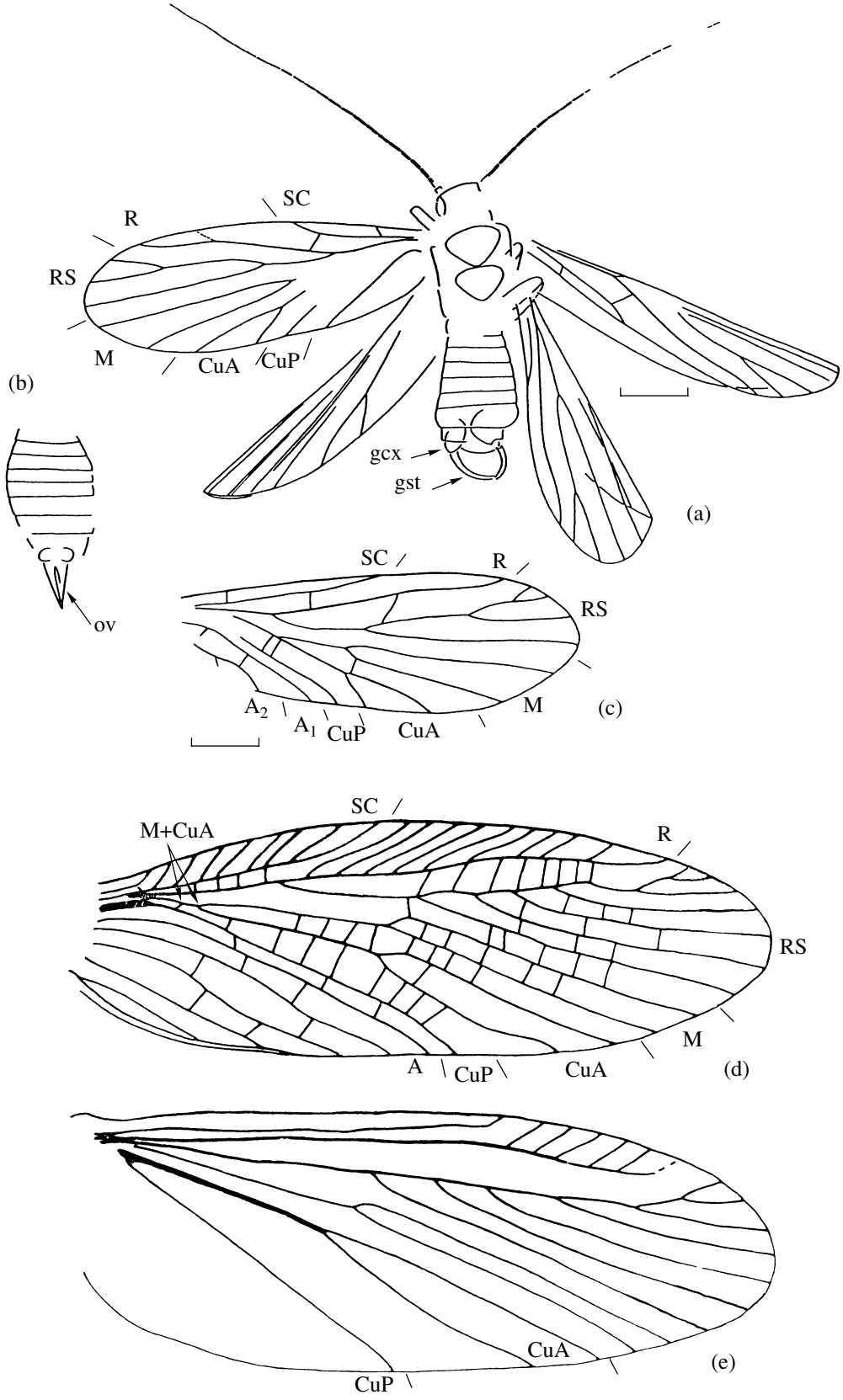

Fig. 2. Miomopterans of the family Palaeomanteidae: (a) and (b) *Delopterum rasnitsyni* Novoksh.: (a) habitus of male, (b) female abdomen with ovipositor (after Novokshonov, 2000); (c) forewing of *Delopterum candidum* Zhuzhg. (after Zhuzhgova, 2002); (d) and (e) fore- and hindwings of *Epimastax sojanensis* (A. Rasn.) (after Rasnitsyn, 1977). Scale bar for Figs. 2a–2c, 1 mm; other figures are out of scale.

markedly curved toward each other; the female abdomen bears a wide (in the dorsal view) and moderately long ovipositor; no cerci have been revealed in the Early Permian species *D. rasnitsyni* Novoksh., 2000 from the Urals. The wings are ovoid and not very elongate; among the venational features, the shortened SC and loss of its anterior branches (except for the humeral vein) are worth mentioning. The photograph in Carpenter (1939, pl. 2, Fig. 3) indicates that *Delopterum* from the Lower Permian of Kansas differs from the species described from the Urals in the broader pronotum and in the presence of short segmented cerci. In addition, short segmented cerci and wings that certainly are folded rooflike have been recorded in several undescribed specimens of *Delopterum* spp. from Tshekarda (the authors' pers. observations). The composition and system of the genus certainly need revision.

The Late Permian genus *Epimastax* is known only from its wings and differs from the other genera of the family in the numerous anterior branches on R (SC here is comparatively short and multibranched), multibranched RS, short M+CuA anastomosis, and having more than three anal veins (Figs. 2d–2e).

The family Permosialidae. This family is characterized by a feature that is unique among miomopterans: their forewings retain a free (even if short) M_5 base that forms a Y-shaped figure at the junction with CuA (presumably a primitive condition!) rather than a subbasal M+CuA anastomosis, except for aberrant specimens, e.g., the holotype of *Permosialis asiatica* O. Mart from the Upper Permian of the Kuznetsk Basin (Martynova, 1961) and some specimens of *Permonka jurassica* A. Rasn. from the Jurassic of Central Asia (Rasnitsyn, 1977) that received no illustrations. The earliest Permosialidae have been discovered in the Lower Permian of the Urals, where they are represented by a single genus, *Permosialis* (Figs. 3a–3d). In the Late Permian of what is now Eurasia, this genus became widespread (Fig. 3e), and its most recent representatives were discovered in the Middle–Upper Triassic of Kyrgyzstan (see the description of new taxa below). *Permosialis* possessed broad forewings with a markedly convex anterior margin, quite long multibranched SC, and a tough membrane; these are the only miomopterans to have a color pattern on their wings consisting of transverse bands and numerous small spots or larger ocellate spots. The body in *Permosialis* is robust (known only from the Tshekarda materials: Novokshonov and Rasnitsyn, 2001); the pronotum is wide; the meso- and metanotum appear narrow compared to the body. None of the 12 complete *Permosialis* specimens collected in the Tshekarda locality have been preserved in the lateral position. Nevertheless, the posterior margins of their forewings never overlap; therefore, one may conclude with some degree of confidence that the wings in *Permosialis* were folded rooflike. Among the distinctive features of this genus, an unusual tarsal structure is worth mentioning: the tarsi appear to be shortened (this being especially noticeable in the hind legs) and, apparently, consist of only three segments. In one instance, three long subapical spurs were discovered on the hind tibia (similar but shorter spurs were figured in *Sellardsiopsis conspicua* G. Zal. (= *Palaeomantisca lata* Mart.) (Rasnitsyn, 1977, p. 76, text-fig. 12a). Probably *Permosialis* species were sexually dimorphic in size. At least, in the Tshekarda materials several small *Permosialis* specimens (forewing 7.5–8.5 mm long) are males (abdomen ending with the swollen genital capsule), while one of the large specimens (forewing 13–14 mm long) is a female with a short ovipositor. Similarly, two size groups of *Permosialis* wings coexist in the other Permian localities, Soyana, Kaltan, and Bor-Tolgoy (Martynova, 1952, 1961; Storozhenko, 1992). These are *P. perfecta* O. Mart. (forewing 18 mm long) and *P. cauleoides* O. Mart. + *P. immaculata* O. Mart + *P. fasciata* O. Mart (forewing 10–13 mm long) in Soyana; *P. sibirica* O. Mart. + *P. asiatica* O. Mart. (forewing 18–20 mm long) and *P. matulina* O. Mart. (forewing 11 mm long) in Kaltan; *P. mongolica* (Storozh.) (forewing 25–30 mm long) and *P. nana* (Storozh.) (forewing about 15 mm long) in Bor-Tolgoy.

The second genus of the family, *Permonka*, appears quite late in the fossil record (Upper Permian of South Africa) and was most abundant in the Triassic and Early Jurassic of Central Asia (Figs. 3f–3g). Of the characters unique to miomopterans, the most important is wings that are folded flat (Rasnitsyn, 1977). Only one more or less complete specimen (an undescribed male) of this genus is known (from the Triassic of Kazakhstan, Kenderlyk locality); the other localities have yielded only wings, often broadly overlapped. The gonostyles of this male are not shortened, quite wide, and not curved (the authors' pers. observ.; also Rasnitsyn, 2002, p. 164, text-fig. 208); the meso- and metanotum are subdivided as usual.

The family Palaeomantiscidae. This family is known only from the Lower Permian of the Urals (Rasnitsyn, 1977). Two monotypic genera included in the family show a rooflike wing folding and an identical SC structure (SC terminates on R instead of the anterior wing margin). The genus *Sellardsiopsis* (Fig. 4a) is characterized by jumping hind legs and a four-segmented tarsus; the ovipositor is short and wide in profile; the gonostyles are slender, long, and curved (Rasnitsyn, 1977). The genus *Palaeomantina* (Figs. 4b–4d; Pl. 10, Fig. 1) shows ***elongate mandibles*** (undescribed PGU specimen), unmodified hind femora (i.e., legs non-jumping!), ***five-segmented tarsus, distinct anal loop*** in the forewings (A_2 terminating on A_1; structure of A_3 unknown), and also anastomosis of the anterior M branch with RS and ***convex CuA in hindwings***; the ovipositor is short; the male genitalia are small, with fingerlike short gonostyles. An incipient anal loop and short RS+M_1 anastomosis occur also in the forewings of some Palaeomanteidae (Martynova, 1961; Kukalová, 1963), but all the characters in bold italic type are unique to the order; thus, one cannot exclude that the genus *Palaeomantina* deserves to be separated at the family level.

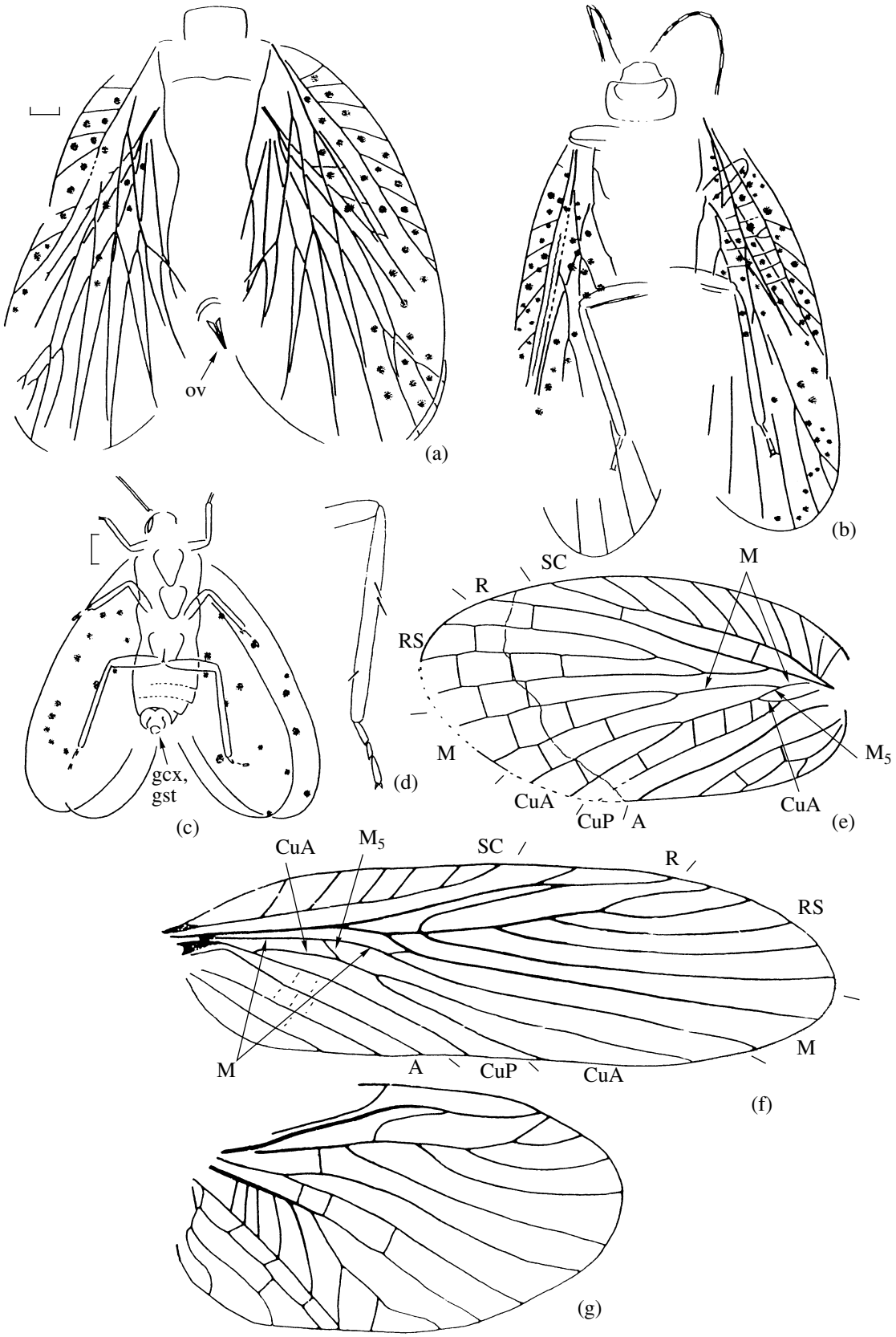

Fig. 3. Miomopterans of the family Permosialidae: (a)–(d) *Permosialis punctimaculosa* Novoksh. et A. Rasn.: (a) and (b) females, (c) male, (d) hind leg (after Novokshonov and Rasnitsyn, 2001); (e) forewing of *Permosialis sibirica* O. Mart. (after Martynova, 1961); (f) and (g) fore- and hindwings of *Permonka triassica* A. Rasn. (after Rasnitsyn, 1977). Scale bar for Figs. 3a–3c 1 mm; other figures are out of scale.