

Permosialidae (Insecta: Palaeomanteida): Composition, Systematics and Relationships

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Received June 13, 2023; revised July 5, 2023; accepted July 5, 2023

Abstract—The composition of the order Miomoptera is considered at the family level, and the system of the family Permosialidae is revised. Keys are provided to families of the order and to genera and species of the family Permosialidae, with synonymies and unified diagnoses of the genera and species of Permosialidae. The composition of the family is shown to remain uniform through its entire time interval, with the type genus always prevalent, and the only one recorded at its start (late Kungurian) and finish (Triassic). The geographical distribution of Permosialidae is noteworthy: widespread over Angarida and confined to that region except for a unique record from Australia.

Keywords: Miomoptera, Palaeomanteida, Epimastacidae, Permonkidae, Permembidae, Angarida

DOI: 10.1134/S0031030124010052

INTRODUCTION

The first representative of the extinct, predominantly Permian family Permosialidae, *Permosialis paucinervis* Martynov, 1928, was described by Martynov (1928) in the order Megaloptera, and a closely related species (*Palaeomantopsis furcatella* Martynov, 1928) was assigned to Miomoptera incertae sedis. Later, Permosialidae were variously assigned, e.g., to the order Megaloptera (Martynov, 1933; Martynova, 1952, 1961, 1962), insects of unclear position (Carpenter, 1992) or the order Palaeomanteida (=Miomoptera) (Rasnitsyn, 1980a, 1980b, 2002; Novokshonov and Zhuzhgo, 2004; Rasnitsyn and Aristov, 2013). Representatives of the family Permosialidae in the sense of this paper were described by Martynov (1928, 1933), Martynova (1952, 1961), Riek (1968), Storozhenko (1991, 1992a, 1992b); Storozhenko and Novokshonov (1999); Novokshonov and Rasnitsyn (2001); and Novokshonov and Zhuzhgo (2004), Rasnitsyn and Aristov (2013); Aristov and Rasnitsyn (2022); Aristov and Rasnitsyn (2023a, 2023b). With this paper we complete the revision of the family begun in the last two listed publications.

TAXONOMIC BOUNDARIES AND SYSTEMATICS OF THE FAMILY PERMOSIALIDAE

The taxonomy and boundaries of the family Permosialidae are still not resolved. The family was estab-

lished in the order Megaloptera with two species in a single genus (Martynov, 1928) and then transferred by Riek to the order Miomoptera (=Palaeomanteida Rohdendorf, 1977) (Riek, 1976). It quickly increased in size due to new descriptions (Martynova, 1952, 1961; Riek, 1968; Novokshonov and Rasnitsyn, 2001; Rasnitsyn and Aristov, 2013; Aristov and Rasnitsyn, 2022; Aristov and Rasnitsyn, 2023a, 2023b) and with the transfer of species from other orders of insects (Storozhenko and Novokshonov, 1999). The number of genera also increased: Riek (1976) included three genera: *Permosialis* Martynov, 1928, *Permonikia* Kukalová, 1963 and *Permonka* Riek, 1976. Rasnitsyn (1977) first included two genera in the Permosialidae (*Permosialis* and *Sindomioptera* Rasnitsyn, 1977 = *Epimastax* Martynov, 1928), then five (Rasnitsyn, 1980a: *Permosialis*, *Epimastax*, *Permonka*, *Permonia* Kukalová, 1963 and *Permonikia* Kukalová, 1963). Storozhenko and Novokshonov (1999) included seven genera: *Permosialis*, *Epimastax*, *Permonka* Riek, 1973 (= *Perloblatta* Storozhenko, 1992), *Permonia*, *Permonikia*, *Sarbalopterodes* Storozhenko, 1991 and *Tologoptera* Storozhenko, 1992. The last two genera were later synonymized with *Permosialis* (Rasnitsyn and Aristov, 2013). Rasnitsyn and Aristov (2013) also added two more genera here, *Balymotikha* Rasnitsyn et Aristov, 2013 and *Onthomastax* Rasnitsyn et Aristov, 2013. Finally, Aristov and Rasnitsyn (2023a) transferred the genus *Palaeomantopsis* Martynov, 1928 to Permosialidae from Palaeomanteidae. On the other hand, Carpenter (1992, p. 501) still did not recognize the family Permosialidae and assigned the genus *Permosialis* to

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Neoptera: order uncertain. Views on the position of the family within the system changed equally whimsically. As already mentioned, permosialids were described as part of the order Megaloptera and remained part of it for a long time, until Riek (1976) and Rasnitsyn (1977) independently substantiated their assignment to the order Miomoptera (=Palaeomanteida). This order originally (Martynov, 1927) included six families, which were later recognized as unrelated: Palaeomantidae Handl. (=Palaeomanteidae), Delopteridae Sell. (=Palaeomanteidae), Lecoriidae Handl. (=Lemmatophoridae), Lemmatophoridae Sell., Probnisidae Sell., Liomopteridae Sell. (Carpenter, 1992; Rasnitsyn and Aristov, 2013; Aristov, 2015). These families, except for the first two, have now been transferred to the forgotten extinct order Reculida Handlirsch, 1806, which represents one of the groups of lower gryllonean insects (Gryllones = Polyneoptera) and unites a significant part of the former order Paraplecoptera (Aristov, 2015).

Tillyard (1928) did not recognize Miomoptera and insisted that Delopteridae were close to Psocoptera, and not to Paraplecoptera, which at that time included Lemmatophoridae Handlirsch, 1906, Liomopteridae Sellards, 1909 and Probnisidae Sellards, 1909 (Aristov, 2015). Later, Martynov (1937) and Carpenter (1939) accepted this point of view (Martynov retained the order Miomoptera in the same composition). In the same years, Tillyard (1937) included his new family Permembiiidae Tillyard, 1937 in Miomoptera: this decision, which met with objections (e.g., Martynova, 1961), was subsequently confirmed (Kukalová, 1963; Aristov and Rasnitsyn, 2009).

The family Archaeomiopteridae Güthorl, 1939 (Güthorl, 1939) was also added to the order Miomoptera; this proposal was initially accepted (Martynova, 1961, 1962; Carpenter, 1992), but then abandoned due to insufficient preservation of the only known imprint of *Archaeomioptera carbonaria* Güthorl, 1939 (Rasnitsyn, 1980a, 1980b). Carpenter also assigned to Miomoptera the family Metropatoridae Handlirsch, 1906, which differs considerably from the rest of the Miomoptera (except Archaeomiopteridae) in its dichotomous RS (Carpenter, 1992). This proposal also did not find support among subsequent authors.

Rasnitsyn (1977) described two families in the Miomoptera (Permonkidae Rasnitsyn, 1977 and Palaeomantiscidae Rasnitsyn, 1977), and in the family Permosialidae—the genus *Sindomioptera* Rasnitsyn, 1977, which was shown to be synonymous with *Epimastax* Martynov, 1928, the type genus of the family Epimastacidae Martynov, 1928 (Rasnitsyn, 1980a). Subsequently, Rasnitsyn repeatedly changed his opinion about the status of the above families and about the taxonomy of the order Miomoptera. In 1980–2002 he recognized three families in the order: Palaeomantidae, Permosialidae (including Epimastacidae Martynov, 1928 and the family Permonkidae recently estab-

lished by him) and Palaeomantiscidae (Rasnitsyn, 1980a, 1980b, 2002). In 2009, the family Permembiiidae, which was shown to be very diverse, was restored within the order (Aristov and Rasnitsyn, 2009), and in 2013, the entire diversity of the order was again reduced to three families: Palaeomantidae (including Palaeomantiscidae), Permosialidae (including Epimastacidae, Permonkidae, Perloblattidae Storozhenko, 1992 and Tologopteridae Storozhenko, 1992) and Permembiiidae, due to insufficient knowledge of the order. Prokop et al. (2017) took the radical step of removing all families from the order, except the type family, but without specifying the position in the system of the excluded families. At the same time, they described two new genera, differing from all Miomoptera by a dichotomous RS (as in Metropatoridae, see above), and assigned them to Palaeomantidae, a decision difficult to agree with.

The above clearly shows the need to revise not only the structure of the family Permosialidae, but also the composition of the order Palaeomanteida. In this case, the revision of the order involves formulating its diagnosis, and determining the composition of its families and their diagnoses. Clarification of the phylogenetic relationships of families and genera currently seems premature.

Order Palaeomanteida Handlirsch, 1906

D i a g n o s i s. Sizes from small to large (forewing length 2–26 mm). Eyes known to be large to moderately small. Antennae polysegmented (in some cases with more than 10 segments), filamentous or setaceous, without obvious specializations. Mouthparts chewing. Prothorax and metathorax not reduced (each is longer than half of the mesothorax). Mesoventropleuron with discrimen (mesosternum invaginated), middle coxae contacting each other. Legs short to very long and thin; hind legs sometimes adapted for jumping (with very thickened femora), tarsi are four-segmented, less often three- or five-segmented. Resting position of wings roof-like, sometimes low roof-like with the anterior edges widely diverging backwards, rarely flat with parallel anterior edges on the right and left. Wings are similar in length, heteronomous, usually with moderately depleted venation, forewings are often spotted (sometimes ocellated) or banded, rarely darkened or with a more complex pattern. In forewing, costal and subcostal areas are moderately wide to moderately narrow. Pterostigma usually weak or absent, rarely large. SC is short to very long, usually flowing into C, often with numerous anterior branches. R with R1 sometimes bearing numerous anterior branches, and pectinate RS. M at base with M₅ or at some distance fused with CuA, bifurcating, but anterior branch sometimes continuing to RS as its posterior branch. CuA biramous or simple, very rarely with three short branches, usually convex, but sometimes its stem and/or branches

slightly concave (not as sharply as in hind wing). Anal region often forming separate clavus, with anterior margin highly elevated above the concave CuP; with from two to five anal veins. Simple crossveins can be numerous, but often poorly preserved. Hind wings usually of similar structure, distinguished by narrow costal and subcostal areas, very early origin of RS, always clearly concave CuA, absence of clavus and sometimes slightly expanded anal area. Abdomen without distinct specializations, ovipositor with third valves forming a sheath. Male genitalia with large gonocoxae and movable gonostyli. Short segmented cerci present.

Composition. Families Palaeomanteidae Martynov, 1928 (Late Carboniferous–Late Permian), Permosialidae Martynov, 1928 (Early Permian–Late Triassic), Epimastacidae Martynov, 1928 (Permian), Permonkidae Rasnitsyn, 1977 (Late Permian–Late Jurassic) and Permembidae Tillyard, 1937 (Permian). To differentiate them, see the key below.

Remarks. *Forcinerva tongchuanensis* Hong et Guo, 2003, described from the Middle Triassic (Ladinian Stage) of Shanxi (China) in the family Mesopanorpididae (Mecoptera) (Hong and Guo, 2003) also most likely belongs to the order Palaeomanteida and, possibly, to the family Permosialidae. There are certain doubts (in addition to the insufficient quality and incorrect interpretation of the images) concerning the fact that, judging from the photograph, SC here is shorter than that of known permosialids. The assignment of the genus *Forcinerva* Hong et Guo, 2003 to Permembidae is excluded by the biramous CuA, the assignment to Permonkidae is doubtful due to the non-narrowing (contrary to the figure) costal field, and to Epimastacidae due to the probable absence of the comb of the anterior branches of R. A more reliable identification of *Forcinerva* requires study of the holotype.

The concept of the phylogenetic position of the order Palaeomanteida as a basal group of insects with complete metamorphosis, substantiated by Rasnitsyn (1980a; 2002), remains valid: in our opinion, the data accumulated since then do not contradict this. The diagnostic differences of the order from other insects with complete metamorphosis are also formulated there—primarily, the ovipositor fully formed, as in Hymenoptera, but with a completely different wing venation (combed RS and two-branched M and Cu).

Since the last revision (Aristov and Rasnitsyn, 2009), the extensive family Permembidae has only been supplemented by two monotypic genera (Rasnitsyn and Aristov, 2013). The families Epimastacidae and Permonkidae are monotypic and require revision at the species level. A revision of the largest family Palaeomanteidae is urgently needed, but at present remains too complex, so here we will limit ourselves to an analysis of the composition and structure of the family Permosialidae. An analysis of the phylogenetic

relationships of the families also needs to be postponed to the future.

Key to the Families of the Order Palaeomanteida (Based on the Characteristics of the Forewing)

1. CuA simple. Anterior margin of wing is straight, costal area narrow.....Permembidae
— CuA with a fork.....2
2. R with numerous anterior branches, starting at level of the apex of SC, SC not extending beyond mid-wing, often very short. CuA convex.....Epimastacidae
— R at most with one anterior branch at the apex, SC often long.....3
3. Wings folded flat on the back, with parallel leading edges on the right and left. Anterior margin of wing straight or almost straight, costal area moderate or usually quite narrow. M and CuA free (connected M₅). CuA convex.....Permonkidae
— Wings folded roof-like, without wide overlap; if they are low roof-like (almost flat), then their front edges diverge strongly posteriorly. While CuA is convex, M and CuA are fused at a large distance.....4
4. M + CuA long (comparable in length to M and CuA stems). CuA convex.....Palaeomanteidae
— M + CuA short or (usually) absent. CuA concave....
.....Permosialidae

Family Permosialidae Martynov, 1928

Permosialidae: Martynov, 1928, p. 93; Martynova, 1961, p. 470; 1962 p. 269; Rasnitsyn, 1980a, p. 37; Storozhenko and Novokshonov, 1999, p. 2; Rasnitsyn and Aristov, 2013, p. 690.

Type genus. *Permosialis* Martynov, 1928.

Diagnosis. Wings wide, fold low and roof-like when at rest. In forewing, costal area moderately wide, SC extends far beyond the mid-wing, with anterior branches, R simple or, rarely, with one anterior branch, RS with three to four branches, M with M₅ or fused with CuA in a short segment, CuA usually concave (often not entirely), biramous; clavus relatively weakly expressed. In hind wing, intercubital field not expanded and without thick crossveins; anal area not expanded. Tarsus three-segmented.

Composition. *Permosialis* Martynov, 1928 (Early Permian–Late Triassic), *Palaeomantopsis* Martynov, 1928 (Middle–Late Permian), *Balymotikha* Rasnitsyn et Aristov, 2013 (Late Permian), *Onthomas-tax* Rasnitsyn et Aristov, 2013 (Late Permian).

Comparison. See key to families.

Remarks. The wide distribution of the family as a whole, and its type genus in Angarida (from the east of the European part of Russia to Mongolia and China), is noteworthy. In the Middle and Late Permian, permosialids were found here quite regularly, but were not recorded anywhere else, except for a single

find in Australia. Note that the family did not become extinct at the Permian-Triassic boundary. Only the type genus, with a single species, the most abundant in the Permian, continued into the Triassic; no new genera arise.

Key to the Genera of Permosialidae
Based on a Forewing

1. Fork of M at base of RS (Fig. 2j).....*Balymotikha*
– Fork of M near fork of RS.....2
2. Fork of CuA much more basal than base of RS (Fig. 2k).....*Onthomastax*
– Fork of CuA near or usually distal to base of RS.....3
3. RS three-branched (Figs. 1a – 1m; Figs. 2a–2i).....*Permosialis*
– RS four-branched (Figs. 2l – 2n)....*Palaeomantopsis*

Genus *Permosialis* Martynov, 1928

Permosialis: Martynov, 1928, p. 94; Martynova, 1952, p. 228; 1961, p. 470; 1962, p. 270; Carpenter, 1992, p. 501; Storozhenko and Novokshonov, 1999, p. 4; Rasnitsyn and Aristov, 2013, p. 691.

Sarbalopterodes: Storozhenko, 1991, cp. 110 (type species *S. frivolus* Storozhenko, 1991); Storozhenko and Novokshonov, 1999, p. 3; Rasnitsyn and Aristov, 2013, p. 691.

Tologoptera: Storozhenko, 1992b, p. 126 (type species *T. mongolica* Storozhenko, 1992); Rasnitsyn and Aristov, 2013, p. 691.

Type species. *Permosialis paucinervis* Martynov, 1928.

Diagnosis. Front wing with three-branched RS. Forks of M and CuA near or distal to the base of RS.

Composition. *P. asiatica* Martynova, 1952, *P. bayda* Aristov et Rasnitsyn, 2022, *P. belebei* Aristov et Rasnitsyn, 2022, *P. belmontensis* Riek, 1968, *P. frivola* (Storozhenko, 1991), *P. latiformis* Martynova, 1952, *P. martynovae* Aristov et Rasnitsyn, 2023, *P. matutina* Martynova, 1961, *P. mongolica* Aristov et Rasnitsyn, 2023, *P. paucinervis* Martynov, 1928, *P. perfecta* Martynova, 1952, *P. postumus* Aristov et Rasnitsyn, 2023, *P. punctimaculosa* Novokshonov et Rasnitsyn, 2001, *P. triassica* Novokshonov et Zhuzh-gova, 2004, *P. ualentovae* Novokshonov et Zhuzh-gova, 2004, *P. udmurtensis* Rasnitsyn et Aristov, 2013, *P. virgata* Aristov et Rasnitsyn, 2023b, *P. vizzya* Aristov et Rasnitsyn, 2023, *P. zavialovensis* Rasnitsyn et Aristov, 2013 from the Permian (Kungurian–Vyatkian) and Triassic (Carnian and probably Ladinian) Russia, Kazakhstan, Kyrgyzstan, Mongolia and Australia (see below for details).

Comparison. See the key for the genera.

Key to the Species of the Genus Permosialis Based on the Forewing (P. latiformis Martynova, 1952, known only from the hindwing is not included)

1. Stem and branches of CuA near fork and CuP at apex are angularly curved at confluence of cross-

- veins. Anterior margin of wing in 2nd and 3rd quarters straight and parallel to posterior margin. First fork of RS in distal third of wing. Forewing length 13.5 mm (Fig. 1f).....*P. belmontensis*
- CuA and CuP smoothly curved at confluence of crossveins (rarely CuP kinked). Anterior margin of wing rarely straight, first fork of RS rarely in distal third of wing.....2
2. Branches of SC long.....3
– Branches of SC similar in length to distance between them.....5
3. Stem of RS₁₊₂ moderately long, so fork RS₁₊₂ is further than mid-wing. Forewing length 16–22 mm (Fig. 1e).....*P. belebei*
– Stem of RS₁₊₂ very short, fork RS₁₊₂ before mid-wing.....4
4. R in distal third concave and distinctly weakened. Forewing length 25.2–26.5 mm (Fig. 1l).....*P. mongolica*
– R convex, clear almost to apex. Forewing length 19 mm (Fig. 1c).....*P. asiatica*
- 5(2). First RS and M forks in first third of wing. Forewing length 17.6 mm (Figs. 2c, 2d).....*P. triassica*
– First RS and M forks in second third of wing.....6
6. Anterior margin of wing straight behind base of SC. Stem of RS₁₊₂ short (clearly shorter than RS stem and less than half length of RS₁). Short M + CuA developed. Coloration variable, often with large, often contacting, rimmed spots on a darkened background, but varying from complete absence or traces in the form of streaks to wide uneven darkening. Forewing length 21.6 mm (Figs. 1g, 1h).....*P. frivola*
– Forewing convex. Coloring, if expressed, is different...7
7. Wing with clear, elongated dark spots marking the crossveins (Fig. 2i).....*P. zavialovensis*
– Wing without such spots.....8
8. RS₁ very short, no longer or barely longer than distance from its apex to apex of R. Wing with small dark round spots of approximately same size (half the width of most spaces between veins). Forewing length 7.5–13.5 mm (Fig. 2b).....*P. punctimaculosa*
– RS₁ clearly longer. Spots, if developed, larger or of different sizes.....9
9. Stem of RS₁₊₂ one third length of RS₁. Wing with ocellated (bordered) spots. Forewing length about 16 mm (Fig. 2e).....*P. ualentovae*
– Stem RS₁₊₂ not shorter than half of RS₁.....10
10. Stem RS shorter than half of stem of RS₁₊₂. Wing with light spots on dark background. Forewing length about 25 mm (Fig. 1d).....*P. bayda*
– Stem RS longer than half of stem of RS₁₊₂. Wing coloration is different.....11
11. In the intercubital field, a powerful oblique crossvein to the CuA fork, CuP is kinked when

- meets it. Dark base of the wing and stripe connected by a darkened costal area. Forewing length about 12–13 mm (Fig. 2g).....*P. virgata*
- Intercubital field without a thick crossvein. Costal field in the middle part is not darkened.....12
12. Wing with clear, approximately equal-sized, spaced ocellated spots. Fork of CuA at its base much narrower than fork of M. Forewing length 15–18 mm (Fig. 1m).....*P. perfecta*
- Wing without ocellate spots of standard size. Fork of CuA at base rarely noticeably narrower than fork of M.....13
13. Wing with rounded dark spots, forming a transverse stripe before apex. Forewing length 10.2 mm (Fig. 1j).....*P. martynovae*
- Wing without regular spots, with stripes or light-colored, sometimes with irregular darkening.....14
14. Base of wing and stripe from forks of RS, M and CuA to fork RS₁₊₂ darkened. Forewing length about 11 mm (Fig. 1k).....*P. matutina*
- Base of wing light-colored.....15
15. Stripes reach anterior margin of wing. Forewing length 10.5 mm (Fig. 2h).....*P. vizzya*
- Stripes absent or do not enter costal field.....16
16. Wing in the distal third narrowed strongly and almost in straight line toward a narrowly rounded apex. Forewing length 17 mm (Fig. 2f).....*P. udmurtensis*
- Wing is weaker tapered to broadly rounded apex.....17
17. First RS fork before mid-wing, RS stem almost straight. Forewing length 11.4–14.6 mm (Fig. 2a).....*P. postuma*
- First RS fork after mid-wing, RS stem clearly arched back. Forewing length 9.0–13.5 mm (Figs. 1a, 1b).....*P. paucinervis*

Permosialis paucinervis Martynov, 1928

Permosialis paucinervis: Martynov, 1928, p. 94, pl. 8, figs. 4, 5, pl. XV, figs. 3; Martynova, 1952, p. 229; Carpenter, 1992, p. 501; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1, pl. 8, figs. 1–9.

Permosialis bifasciata: Martynov, 1933, p. 74, text-fig. 9; Martynova, 1952, p. 234; 1962, p. 269, text-fig. 843; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1b, pl. 8, fig. 2.

Permosialis defurcata: Martynova, 1952, p. 230, text-fig. 25; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1h, pl. 8, figs. 8.

Permosialis brevifurcata: Martynova, 1952, p. 230, text-fig. 26; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1i, pl. 8, fig. 9.

Permosialis cauleoides: Martynova, 1952, p. 233, text-fig. 29; Novokshonov and Zhuzhgova, 2004, p. 177; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1v, pl. 8, fig. 3.

Permosialis marmorata: Martynova, 1952, p. 234, text-fig. 30; Novokshonov and Zhuzhgova, 2004, p. 177; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1g, pl. 8, fig. 4.

Permosialis immaculata: Martynova, 1952, p. 235, text-fig. 31; Novokshonov and Zhuzhgova, 2004, p. 177; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1d, pl. 8, fig. 5.

Permosialis fasciata: Martynova, 1952, p. 236, text-fig. 32; Novokshonov and Zhuzhgova, 2004, p. 177; Aristov and Rasnitsyn, 2023a, p. 70, text-fig. 1e, pl. 8, fig. 6.

H o l o t y p e. Russia, Tatarstan, right bank of the Kama River at the Tikhye Gory pier, location of Tikhye Gory; Middle Permian, Kazanian Stage, Lower Kazanian Substage, Baitugan Formation, *Lingula* Beds. Holotype was not found, probably lost. Interpretation of the species is based on the original description and image.

D e s c r i p t i o n (Figs. 1a, 1b). The forewing has a broadly rounded apex. The wing anterior margin is convex. The SC branches are not long (commensurate with the distance between them). R is convex and distinct almost to the apex. Stem RS is longer than the RS₁ and is clearly curved backwards. The first RS fork is behind the mid-wing. The fork of RS₁₊₂ is before the mid-wing. RS₁ is clearly longer than the distance from its apex to the apex of R. The fork of M is near mid-wing. M₅ is developed. Forks of M and CuA are approximately equal in width at base. CuA and CuP are smoothly bent at the confluence of the crossveins (rarely CuP with a kink). Wing with two stripes or light colored, the stripes do not extend into the costal area, the base of the wing is light. The hindwing 2.3 times as long as wide, the fork of RS₁₊₂ is less than a third of the length of RS, the fork of M is near the mid-wing, the fork of CuA is short.

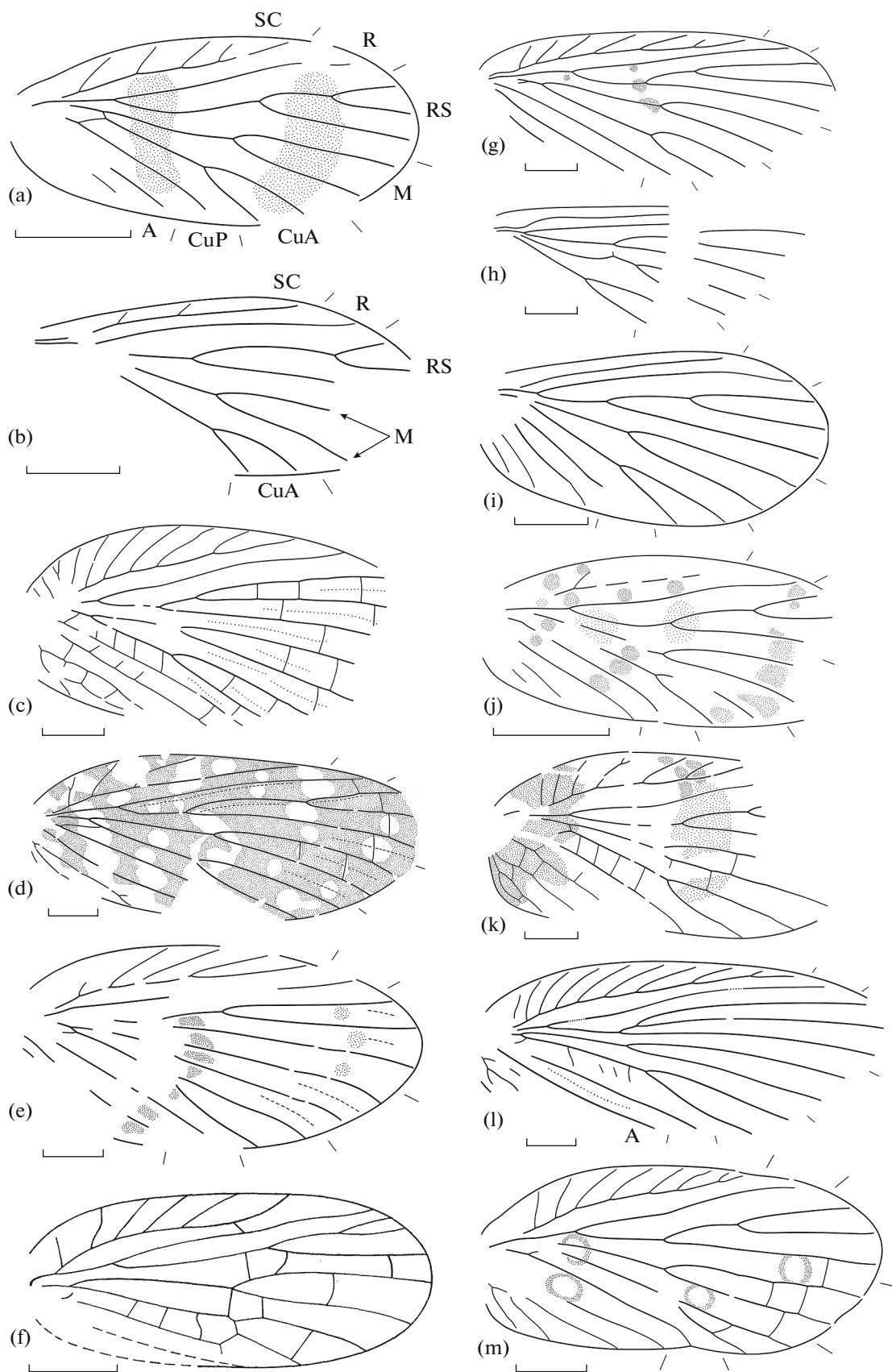
M e a s u r e m e n t s in mm: length of the forewing 9.0–13.5, hindwing 11–13.

C o m p a r i s o n. See the key.

O c c u r r e n c e. Middle Permian (Lower Kazanian); Russia, Arkhangelsk Region and Tatarstan.

M a t e r i a l. In addition to the holotype, 8 specimens from the Ivagora Formation of the Soyana River (Arkhangelsk Region). For more details, see Aristov and Rasnitsyn (2023a).

Fig. 1. Species of the genus *Permosialis* Martynov, forewings (unless otherwise stated): (a, b) *P. paucinervis* Martynov, 1928: (a) forewing, specimen PIN, no. 94/798 (holotype of *P. cauleoides* Martynova, 1952), (b) hindwing, specimen PIN, no. 117/1756 (holotype of *P. brevifurcata* Martynova, 1952); (c) *P. asiatica* Martynova, 1961, specimen PIN, no. 966/16 (holotype of *P. sibirica* Martynova, 1961); (d) *P. bayda* Aristov et Rasnitsyn, 2022, holotype PIN, no. 3701/2; (e) *P. belebei* Aristov et Rasnitsyn, 2022, holotype PIN, no. 1366/379; (f) *P. belmontensis* Riek, 1968, holotype F-40700; (g, h) *P. frivola* (Storozhenko, 1991), specimen PIN, no. 2781/241: (g) forewing, (h) hindwing; (i) *P. latiformis* Martynova, 1952, holotype PIN, no. 117/1153, hindwing; (j) *P. martynovae* Aristov et Rasnitsyn, 2023, holotype PIN, no. 3353/811; (k) *P. matutina* Martynova, 1961, specimen PIN, no. 1197/412; (l) *P. mongolica* (Storozhenko, 1992), holotype PIN, no. 4305/286; (m) *P. perfecta* Martynova, 1952, holotype PIN, no. 117/1772. Scale bar 3 mm.



Permosialis asiatica Martynova, 1961

Permosialis asiatica: Martynova, 1961, p. 471, text-fig. 419, pl. 33, fig. 233.

Permosialis sibirica: Martynova, 1961, p. 471, text-figs. 417, 418, pl. 33, figs. 231, 232; Aristov and Rasnitsyn, 2023b, p. 67.

Holotype. PIN, no. 1197/415, part and counterpart of an almost complete forewing; Russia, Kemerovo Region, Kuzedeevsky District, Kondoma River near the village of B. Kaltan; Middle Permian, Kazanian Stage, Upper Kazanian Substage, Kuznetsk Formation.

Description (Fig. 1c). The forewing with a broadly rounded apex. The anterior margin of the wing is convex. The SC branches are much longer than the distance between them. R is convex and distinct almost to the apex. Stems RS and RS_{1+2} are short, together much shorter than the fork of RS_{1+2} , weakly curved. Forks RS, M and CuA almost at the same level before the mid-wing. The fork of RS_{1+2} is very long (about two thirds of the total RS). RS_1 much longer than the distance from its top to the top of R. M and CuA near the base are fused for a short distance (M_5 not present). The fork of CuA at the base is not narrower than M. Branches CuA and CuP with no kink. The wing color has not been preserved. The hindwing is similar to the front wing due to its short stems RS, RS_{1+2} , M and CuA (all far before the mid-wing).

Measurements in mm: forewing length 18.8–19.3, width 9.5–10.

Comparison. See key.

Material. Holotype, specimen no. 966/16 (18) (holotype *P. sibirica*) and another five specimens from the type locality.

Permosialis bayda Aristov et Rasnitsyn, 2022

Permosialis bayda: Aristov and Rasnitsyn, 2022, p. 21, text-figs. 7, 8.

Holotype. PIN, no. 3701/2, counterpart imprint of forewing; Russia, Kemerovo Region, Novokuznetsk District, Baidaevesky Field, Sample 32/1611, Borehole 1711, depth 506 m; Middle Permian, Urzhumian Stage, Uskat Formation.

Description (Fig. 1d). The forewing with a broadly-rounded apex. The wing anterior margin is convex. Branches of SC are not long (similar to the distance between them). R is convex and distinct almost to the apex. Stem RS is half the length of the stem of RS_1 , strongly bent at the base. Stem RS_{1+2} clearly curved, longer than the fork of RS_{1+2} . RS_1 much longer than the distance from its top to the top of R. M_5 is present. CuA and CuP without kinks, forks CuA at the base wider than fork of M. The wing is dark, with numerous round and oval light spots, forming five to six indistinct transverse stripes.

Measurements in mm: forewing length about 25.

Comparison. See key.

Material. Holotype.*Permosialis belebei* Aristov et Rasnitsyn, 2022

Permosialis ualentovae: Novokshonov and Zhuzhgov, 2004, p. 183, text-fig. 6b (part., only paratypes 1366/379, 1366/463).

Permosialis belebei: Aristov and Rasnitsyn, 2022, p. 19, text-figs. 3–6.

Holotype. PIN, no. 1366/379, counterpart imprint forewing; Russia, Kirov Oblast, Malmyzhsky District, left bank of the Kityak River opposite the village of B. Kityak; Middle Permian, Upper Kazanian, Belebei Formation.

Description (Fig. 1d). The forewing is relatively strongly narrowed towards the apex. The anterior margin of the wing is convex. SC branches are much longer than the distances between them. R is convex and distinct almost to the apex. Stem RS is no longer than the RS_1 stem, slightly curved. The first fork of RS is clearly before the mid-wing, at the level of or proximal to the forks of M and CuA. Fork RS_{1+2} is significantly longer than half the length of RS. RS_1 is much longer than the distance from its apex to the apex of R. M_5 is developed. CuA and CuP without a kink, fork of CuA at the base is much narrower than fork of M. On the wing of the holotype there is an arcuate series of small spots from the middle of the stem of RS_{1+2} to the top of the anal region and three weak spots between RS_1 and M_1 .

Measurements in mm: forewing length: holotype 22, paratype fragment length 13.5, estimated total length about 16.

Comparison. See the key.

Material. Holotype and paratype no. 1366/463 from the type locality.

Permosialis belmontensis Riek, 1968

Permosialis belmontensis: Riek, 1968, p. 304, text-fig. 2; 1976, p. 772.

Holotype. Australian Museum, Sydney, F-40700; imprint forewing; Australia, New South Wales near Belmont; Upper Permian, Changhsingian, Upper Newcastle Coal Measures (not examined).

Description (Fig. 1f). The forewing with a broadly rounded apex. The anterior margin of the wing in the two middle quarters is almost straight. SC branches are twice as long as the distance between them. R is distinct to the apex. Stem RS is longer than a fork, almost straight. Forks M and CuA are almost at the same level behind the mid-wing, proximal to RS fork. Stem RS_{1+2} is short, noticeably curved, the fork of RS_{1+2} is very short (not longer than the branches of SC). RS_1 is much longer than the distance from its apex to the apex of R. M_5 is apparently developed. The fork of CuA at the base is not narrower than the fork of M, CuA_1 and CuA_2 near the base and CuP before the

apex with a kink at the confluence of the corresponding crossveins. Coloration unknown.

Measurements in mm: forewing length ca. 13.5, width 5.7.

Comparison. See the key.

Material. Holotype.

Permosialis frivola (Storozhenko, 1991)

Sarbalopterodes frivulus: Storozhenko, 1991, p. 112.

Permosialis frivola: Rasnitsyn and Aristov, 2013, p. 691; Aristov and Rasnitsyn, 2023b, p. 69, text-figs. 2a–2f, 3, pl. 11, figs. 1–5.

Holotype. PIN, no. 2494/31; part imprint of incomplete forewing; Kazakhstan, East Kazakhstan region, Karaungir River at the mouth of Maichat Creek; Upper Permian, Changhsingian, Maichat Formation.

Description (Figs. 1g, 1h). The anterior margin of the wing is almost straight. The SC branches are not long (commensurate with the distance between them). R is convex and distinct almost to the apex. Stem RS is longer than RS₁, strongly to slightly curved. Forks RS, M and CuA more or less at the same level near the mid-wing. Stem RS₁₊₂ is clearly curved and short. RS₁ is much longer than the distance from its apex to the apex of R. M and CuA are fused over some distance, M₅ is not developed. CuA and CuP without kink, fork of CuA at the base is wider than the fork of M. The forewing color, if preserved, is variable, often bright; there are large, rimmed spots, dark spots, darkened or lightened areas along the crossveins, etc. The hindwing also with a shortened stem RS₁₊₂, but with a shortened fork of M and with a stem of M with a kink at the confluence of the crossvein connecting M with the first fork of RS.

Measurements in mm: length of the only sufficiently complete forewing 21.6, width 10.8.

Comparison. See the key.

Material. Holotype and 28 paratypes from the type locality (Aristov and Rasnitsyn, 2023b).

Permosialis latiformis Martynova, 1952

Permosialis latiformis: Martynova, 1952, p. 231, text-fig. 27; Aristov and Rasnitsyn, 2023a, p. 72, text-fig. 1k, pl. 8, fig. 10.

Holotype. PIN, no. 117/1153, counterpart imprint of a hindwing; Russia, Arkhangelsk Region, Soyana location; Middle Permian, Kazanian Stage, Lower Kazanian Substage, Ivagora Formation.

Description (Fig. 1i). The hindwing is twice as long as wide. The fork of RS₁₊₂ is much longer than the stem of RS₁₊₂. Forks of RS, M and CuA are located before the mid-wing, but distal to its first third. The stem of M without a kink.

Measurements in mm: Hindwing length 14.

Comparison. This species is distinct from the known hindwings of other *Permosialis* species: from *P. paucinervis* it differs in the long fork of RS₁₊₂; from

P. frivola it is different in the straight (without a kink) stem M and longer fork of M; from *P. triassica* it is distinct in the more distal position of main forks. In *P. paucinervis*, the fork of RS₁₊₂ is shorter than half of the stem of RS₁₊₂; in *P. frivola*, stem M with a kink at the level of the base of the first fork of RS and fork of M is shortened (located much distal to the RS and CuA bifurcations); in *P. triassica*, all major forks are located within the basal third or even quarter of the wing.

Material. Holotype.

Permosialis martynovae Aristov et Rasnitsyn, 2023

Permosialis martynovae: Aristov and Rasnitsyn, 2023a, p. 74, text-fig. 2g, pl. 9, fig. 5.

Holotype. PIN, no. 3353/811, part imprint of forewing; Russia, Arkhangelsk Region, Mezensky District, bank of the Soyana River near Mount Sheimo, Soyana locality; Middle Permian, Kazanian Stage, Lower Kazanian Substage, Ivagora Formation.

Description (Fig. 1j). The forewing has a broadly rounded apex. The anterior margin of the wing is convex. Branches of SC are not long (similar to the distances between them). R is convex, clear almost to the apex. The stem of RS is longer than the stem of RS₁₊₂, strongly convex backwards. The first fork of RS is in the mid-wing, at the same level with the forks of M and CuA. The stem of RS₁₊₂ is slightly arched forward. The fork of RS₁₊₂ is short, is less than a third of the total length of RS. RS₁ is much longer than the distance from its top to the top of R. The forks of M and CuA at the base approximately equal in width. CuA and CuP without kinks. Coloration in the form of spots of varying width and intensity, forming three indistinct oblique rows before the base of RS, before its first fork and before the wing apex.

Measurements in mm: forewing length 10.2.

Comparison. See the key.

Material. Holotype.

Permosialis matutina Martynova, 1961

Permosialis matutina: Martynova, 1961, p. 473, text-fig. 420, pl. 33, fig. 234.

Holotype. PIN, no. 1197/453, part and counterpart imprints of an incomplete forewing; Russia, Kemerovo Region, Kuzedevsky Districts, Kondoma River, near the village of B. Kaltan; Middle Permian, Upper Kazanian Substage, Kuznetsk Formation.

Description (Fig. 1k). The forewing with a broadly rounded apex. The anterior margin of the wing is weakly convex. The SC branches are much longer than the distance between them. R is convex, distinct almost to the apex. Stem RS is half of RS, strongly curved. Forks of RS, M and CuA are located almost at the same level near the mid-wing. The stem of RS₁₊₂ is slightly longer than its fork, noticeably

curved. RS_1 much longer than the distance from its apex to the apex of R. M_5 is present. Fork of CuA is slightly narrower at the base than fork of M. Branches of CuA and CuP are without a kink. The wing has a darkened base and a stripe extending from the forks of RS, M and CuA to the fork of RS_{1+2} .

Measurements in mm: counterpart imprint 10.3, apparent complete forewing length 11.3, width 5.4.

Comparison. See the key.

Material. Holotype.

Permosialis mongolica (Storozhenko, 1992)

Toloptera mongolica: Storozhenko, 1992, p. 126, text-fig. 4a–4d, pl. 22, figs. 2; Storozhenko and Novokshonov, 1999, p. 4, text-fig. 2.

Permosialis mongolica: Rasnitsyn and Aristov, 2013, p. 691; Aristov and Rasnitsyn, 2023b, p. 67, text-figs. 1a–1g, pl. 10, figs. 1–4.

Holotype. PIN, no. 4305/286, part and counterpart imprints of an incomplete forewing; Mongolia, South Gobi Province, 16 km southeast of Tsogttsetsii Sum, Bor-Tologoi area, 20 km north-northwest from the Tabun-Tologoi quarry, Bor-Tologoi locality; Upper Permian, Wuchiapingian, Tsankhin Formation.

Description (Fig. 1m). The anterior margin of the wing is strongly convex. Branches of SC much longer than the distances between them. R in the distal third is weak, often barely noticeable. The stem of RS is short, slightly curved. The first fork of RS and forks of M and CuA before the mid-wing. The stem of RS_{1+2} is very short, the fork of RS_{1+2} is before the mid-wing. RS_1 is much longer than the distance from its apex to the apex of R. M_5 is present. CuA and CuP are without a kink, forks of M and CuA at the base are approximately the same width. Wing coloration, if noticeable, is in the form of wide transverse stripes.

Measurements in mm: forewing length 25.2–26.5, width 11.3–11.8.

Comparison. See the key.

Material. Holotype, 10 paratypes and two specimens from the type locality but not from the type series (Aristov and Rasnitsyn, 2023b).

Permosialis perfecta Martynova, 1952

Permosialis perfecta: Martynova, 1952, p. 232, text-fig. 28; Novokshonov and Zhuzhgova, 2004, p. 177; Aristov and Rasnitsyn, 2023a, p. 72, text-figs. 2a, 2b, pl. 9, figs. 1, 2.

Holotype. PIN, no. 117/1772, part imprint of forewing; Russia, Arkhangelsk Region, Soyana locality; Middle Permian, Kazanian Stage, Lower Kazanian Substage, Ivagora Formation.

Description (Fig. 1m). The forewing has a broadly rounded apex. The anterior margin of the wing is convex. Branches of SC are longer than the distance between them. R is convex, distinct almost to the apex. The first fork of RS near the mid-wing, on the same level with the forks of M and CuA. The stem of RS is longer than the stem of RS_1 , is slightly curved back. The stem of RS_{1+2} a third shorter than RS_1 , not sharply curved hump-shaped. M_5 is present. CuA and CuP without kinks. Fork of CuA at the base there is much narrower than the fork of M. The wing membrane is dark, the color is in the form of small light edged spots.

Measurements in mm: forewing length 15–18.

Comparison. See the key.

Material. Holotype and specimen PIN, no. 3353/808 from the type locality.

Permosialis postuma Aristov et Rasnitsyn, 2023

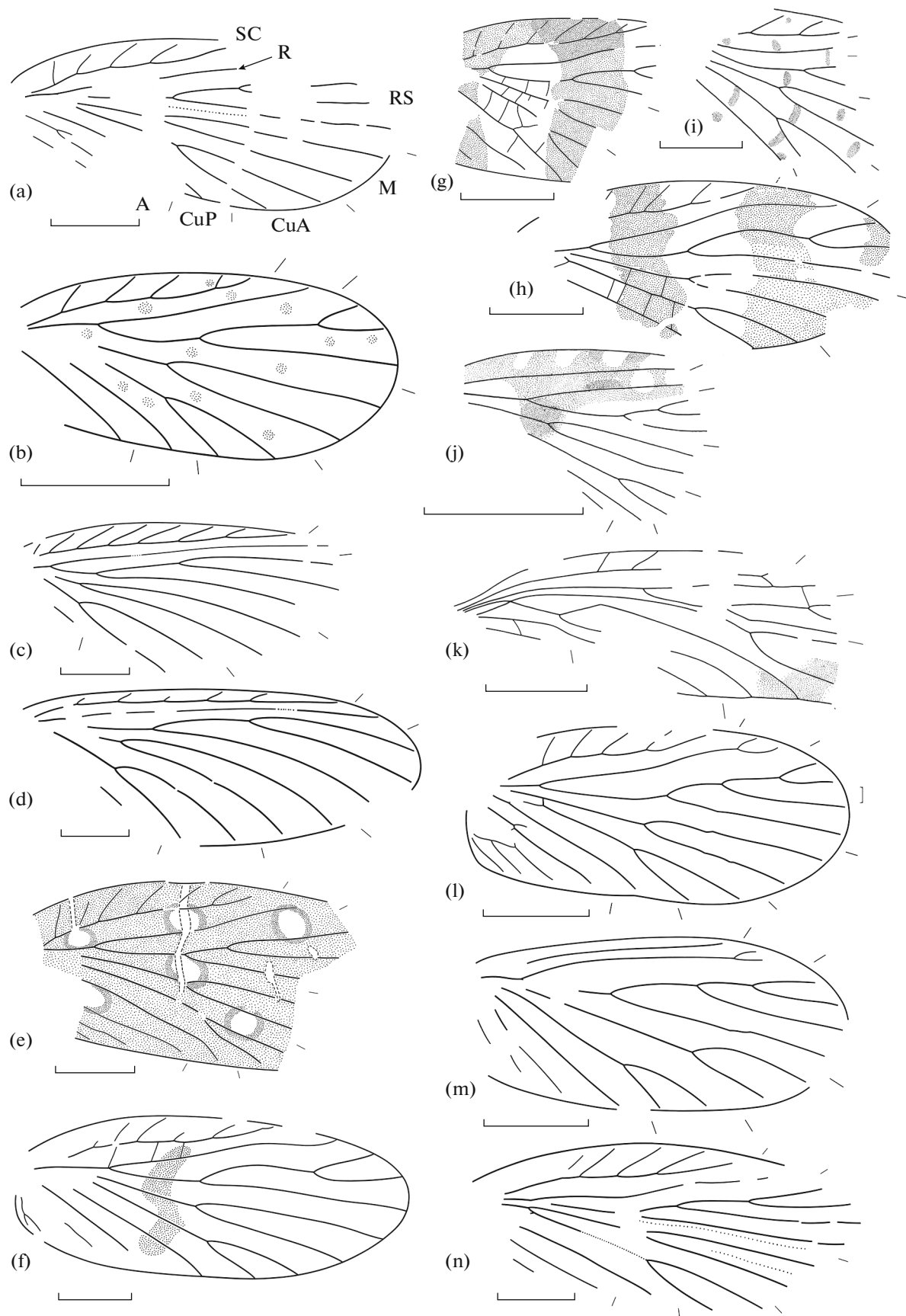
Toloptera nana: Storozhenko, 1992 (part., only paratype no. 4305/321).

Permosialis postuma: Aristov and Rasnitsyn, 2023b, p. 67, text-fig. 1d–1g, pl. 10, figs. 5–7.

Holotype. PIN, no. 4305/321, part and counterpart imprints of an incomplete forewing; Mongolia, South Gobi Province, Bor-Tologoi locality; Upper Permian, Tsankhin Formation.

Description (Fig. 2a). The anterior margin of the wing is convex. The SC branches are not long (less than twice the distance between them). R is distinct almost to the apex. The stem of RS is short, slightly curved. Forks of RS, M and CuA are approximately the same level before the mid-wing. The stem of RS is almost straight, approximately equal in length to stem of RS_{1+2} . RS_1 is much longer than the distance from its apex to the apex of R. CuA and CuP are without a

Fig. 2. Species of the genera *Permosialis* Martynov (a–i), *Balymotikha* Rasnitsyn et Aristov (j), *Onthomastax* Rasnitsyn et Aristov (k), and *Palaeomantopsis* Martynov (l–n), forewings (unless otherwise stated): (a) *P. postuma* Aristov et Rasnitsyn, 2023, holotype PIN, no. 4305/321; (b) *P. punctimaculosa* Novokshonov et Rasnitsyn, 2001, paratype PIN, no. 4987/57; (c, d) *P. triassica* Novokshonov et Zhuzhgova, 2004: (c) forewing, holotype PIN, no. 2555/2066, (d) hindwing, specimen PIN, no. 2555/743; (e) *P. ualentovae* Novokshonov et Zhuzhgova, 2004, holotype PIN, no. 1366/349; (f) *P. udmurtensis* Rasnitsyn et Aristov, 2013, specimen PIN, no. 3286/283; (g) *P. virgata* Aristov et Rasnitsyn, 2023, holotype PIN, no. 4305/279; (h) *P. vizzya* Aristov et Rasnitsyn, 2023, holotype PIN, no. 1631/503; (i) *P. zavialovensis* Rasnitsyn et Aristov, 2013, holotype PIN, no. 3286/124; (j) *B. deterior* Rasnitsyn et Aristov, 2013, holotype PIN, no. 5103/20; (k) *O. coprinus* Rasnitsyn et Aristov, 2013, holotype PIN, no. 3286/146; (l, m) *P. furcatella* Martynov, 1928: (l) forewing, specimen PIN, no. 3353/807, (m) hindwing, specimen PIN, no. 117/1444 (2652) (holotype of *Permosialis quadriramosa* Martynova, 1952); (o) *P. nana* (Storozhenko, 1992), holotype PIN, no. 4305/319. Scale bar 3 mm.



kink. The fork of CuA at its base is not narrower than the fork of M. The wing coloration is not preserved.

Measurements in mm: forewing length holotype 11.4–14.6, width 5.1–5.9.

Comparison. See the key.

Material. Holotype and two paratypes from the type locality.

Permosialis punctimaculosa Novokshonov et Rasnitsyn, 2001

Permosialis punctimaculosa: Novokshonov and Rasnitsyn, 2001, p. 111, text-figs. 1, 2; Novokshonov and Zhuzhgova, 2004, text-figs. 3a–3d.

Holotype. PIN, no. 4987/56 (PU 2/336), part and counterpart imprints of an almost complete insect (without a head); Russia, Perm Region, Suksun District, Sylva River, near the village of Chekarda; Lower Permian, Kungurian Stage.

Description (Fig. 2b). Forewing with a broadly rounded apex. The anterior margin of the wing is convex. The SC branches are not long (similar in length to the distance between them). R is convex almost to apex. The stem of RS is moderately short, curved. The fork of RS is slightly distal to the forks of M and CuA, located at the same level near the mid-wing. The stem of RS_{1+2} is clearly longer than the stem of RS and twice as long as the fork of RS_{1+2} . RS_1 slightly longer than the distance from its apex to apex R. The fork of CuA at the base is slightly narrower than the fork of M. Branches of CuA and CuP without a kink. The wing has numerous small round dark spots.

Measurements in mm: forewing length 7.5–9 in small specimens (males), 13.5 in large (females).

Comparison. See the key.

Material. Holotype and 14 paratypes from the type locality.

Permosialis triassica Novokshonov et Zhuzhgova, 2004

Permosialis triassica: Novokshonov and Zhuzhgova, 2004, p. S183; Aristov and Rasnitsyn, 2023b, p. 70, text-fig. 4.

Holotype. PIN, no. 2555/2066; part and counterpart imprints of an incomplete forewing; Kyrgyzstan, Osh Region, Batken District, Madygen area; Middle or Upper Triassic, Ladinian or Carnian Stage, Madygen Formation.

Description (Figs. 2c, 2d). The anterior margin of the wing is weakly convex or almost straight. The SC branches are not long (similar in length with the distance between them). R is convex and distinct almost to the apex. The stem of RS is short. The forks of RS, M and CuA within the basal quarter or third of the wing. The stem of RS_{1+2} is longer than the stem of R, but shorter than RS_1 . RS_1 is much longer than the distance from its apex to the apex of R. CuA and CuP without a kink, the fork of CuA at the base is wider than the fork of M. The coloration is not preserved.

The hindwing has similar venation, but the stem of RS_{1+2} is usually longer.

Measurements in mm: length of an incomplete forewing of the holotype 14.7, width 7.1, length of specimen no. 2785/3343 17.6, width 6.9.

Comparison. See the key.

Material. Holotype and six paratypes from the type locality (Aristov and Rasnitsyn, 2023b).

Permosialis ualentovae Novokshonov et Zhuzhgova, 2004

Permosialis ualentovae: Novokshonov and Zhuzhgova, 2004, p. 183, text-fig. 6a, pl. 10, fig. 2; Aristov and Rasnitsyn, 2022, p. 2, text-figs. 1, 2.

Holotype. PIN, no. 1366/349, counterpart imprint of the forewing without a base and apex; Russia, Kirov Oblast, Malmyzhsky District, left bank of the Kityak River opposite the village of B. Kityak; Middle Permian, Upper Kazanian, Belebei Formation.

Description (Fig. 2e). The anterior margin of the wing is convex. The SC branches are not long (similar to the distance between them). R convex and distinct almost to apex. The stem of RS is longer than stem of RS_1 , clearly arched back. The first fork of RS is behind the mid-wing, distal to the forks of M and CuA. The fork of RS_{1+2} is very long. RS_1 is clearly longer than its length from its apex to the apex of R. The fork of M is near the mid-wing. CuA and CuP are without a kink, the fork of CuA at the base is much narrower than the fork of M. The wing is darkened, with six large bordered spots, forming three rows at the level of the apex of the stem of RS, the apex of the stem of RS_{1+2} and proximal to the apex of R.

Measurements in mm: forewing fragment length 12.6, estimated total length about 16.

Comparison. See the key.

Material. Holotype.

Permosialis udmurtensis Rasnitsyn et Aristov, 2013

Permosialis udmurtensis: Rasnitsyn and Aristov, 2013, p. 691, text-figs. 13d, 15c.

Holotype. PIN, no. 3286/123, part and counterpart imprints of an incomplete forewing; Russia, Udmurtia, Zavyalovsky District, Rassokha River near the village of Chepanikha; Middle Permian, Urzhumian Stage

Description (Fig. 2f). The forewing is strongly tapered towards the apex. The anterior margin of the wing is convex. The SC branches are not long (similar in length to the distance between them). R is distinct, convex almost to the apex. The stem of RS is much shorter than the stem of RS_{1+2} , almost straight. Forks of RS, M, and CuA almost at the same level near the mid-wing. The stem of RS_{1+2} is long, strongly curved in the basal half, the fork of RS_{1+2} is very short (about a quarter the length of the RS). RS_1 is much longer than the distance from its apex to apex of R. The fork

of CuA at the base is apparently not narrower than the fork of M. The coloration of the wing is poorly preserved.

Measurements in mm: forewing length ca. 17, width 7.8.

Comparison. See the key.

Material. Holotype.

Permosialis virgata Aristov et Rasnitsyn, 2023

Toloptera mongolica: Storozhenko, 1992 (part., only para-type no. 4305/279)

Permosialis virgata: Aristov and Rasnitsyn, 2023b, p. 69, text-fig. 1h, pl. 10, figs. 8.

Holotype. PIN, no. 4305/279, part and counterpart imprints of an incomplete forewing; Mongolia, South Gobi Province, Bor-Tologoi locality; Upper Permian, Tsankhin Formation.

Description (Fig. 2g). The anterior margin of the wing is convex. Branches of SC are not long (similar to the distances between them). R is distally (from the level of the fork of RS_{1+2}) is weak, concave. The stem of RS is longer than the stem of RS_1 , both are curved. The first fork of RS is approximately at the same level with the forks of M and CuA. CuA is without a kink, the fork of CuA is narrower than the fork of M at the base. In the intercubital field there is a powerful oblique crossvein to the CuA fork; CuP is kinked at the place of its origin. The wing has a darkened base and anterior margin and a transverse dark stripe across the stem of RS_{1+2} and further through the basal half fork of M and the fork of CuA.

Measurements in mm: forewing fragment length is about 6.3, width 5.4, estimated total length 12–13.

Comparison. See the key.

Material. Holotype.

Permosialis vizzya Aristov et Rasnitsyn, 2023

Permosialis vizzya: Aristov and Rasnitsyn, 2023a, p. 74, text-fig. 2v, pl. 9, fig. 4.

Holotype. PIN, no. 1631/503, part and counterpart imprints forewing; Russia, Komi Republic, Vorgashorskoye Field, Borehole VK-1349, depth 487 m; Lower Permian, Kungurian Stage (Aristov et al., 2021), Pechora Group, Lekvorkuta Formation, Rudnitskaya Subformation.

Description (Fig. 2h). The forewing has a broadly rounded apex. The anterior margin of the wing is convex. The SC branches are not long (similar in length to the distance between them). R distinct and convex almost to the apex. The stem of RS is shorter than RS_1 , noticeably arched back. The first fork of RS is before the mid-wing, level with the forks of M and CuA. The stem of RS_{1+2} is sharply arched forward. The fork of RS_{1+2} is short, near the wing apex. RS_1 is clearly longer than the distance from its apex to the

apex of R. Forks of M and CuA are of approximately equal width at the base. M_5 is present. CuA and CuP with no kink. The wing with two stripes or light colored, the stripes do not extend into the costal area, the base of the wing is light.

Measurements in mm: forewing length 10.5.

Comparison. See the key.

Material. Holotype.

Permosialis zavialovensis Rasnitsyn et Aristov, 2013

Permosialis zavialovensis: Rasnitsyn and Aristov, 2013, p. 691, text-fig. 13c, 15b.

Holotype. PIN, no. 3286/124, part and counterpart imprints of a forewing fragment; Russia, Udmurtia, Zavialovsky District, Rassokha River near the village of Chepanikha; Middle Permian, Urzhumian Stage.

Description (Fig. 2i). Branches of SC are not long (similar in length to the distance between them). The stem of RS is long and curved. The first fork of RS slightly proximal to the forks of M and CuA. CuA and CuP are without a kink, forks of M and CuA are of similar width at the base. Coloration consists of bright long dark spots arranged in transverse rows along crossveins that are not preserved.

Measurements in mm: forewing fragment length 6.4; width 5.7.

Comparison. See the key.

Material. Holotype.

Genus *Balymotikha* Rasnitsyn et Aristov, 2013

Balymotikha: Rasnitsyn and Aristov, 2013, p. 694.

Type species. *Balymotikha deterior* Rasnitsyn et Aristov, 2013.

Diagnosis. In forewing, anterior branches of SC not present or weak, fork of M located near base of RS, fork of CuA at the level of the first fork of RS, RS at least with three branches.

Species composition. Type species from the Upper Permian of Russia.

Comparison. See the genus key.

Balymotikha deterior Rasnitsyn et Aristov, 2013

Balymotikha deterior: Rasnitsyn and Aristov, 2013, p. 694, text-figs. 14a, 15f.

Holotype. PIN, no. 5103/20, part imprint of a forewing fragment of relatively poor preservation, with no base or apex; Russia, Vladimir Region, Vyazniki, Balymotikha locality; Upper Permian, Vyatkian Stage.

Description (Fig. 2j). See the genus diagnosis.

Measurements in mm: forewing fragment length 6.5; apparent length of the wing ca. 11.

Material. Holotype.

Genus *Onthomastax* Rasnitsyn et Aristov, 2013

Onthomastax: Rasnitsyn and Aristov, 2013, p. 605.

Type species. *Onthomastax coprinus* Rasnitsyn et Aristov, 2013.

Diagnosis. Anterior margin of forewing weakly convex. Branches of SC shorter than distance between them. M and CuA fused at short distance (M_5 not present). Fork of M slightly distal to the first fork of RS. Fork of CuA far basal to base of RS.

Species composition. Type species from the Middle Permian of Russia.

Comparison. See the genus key.

***Onthomastax coprinus* Rasnitsyn et Aristov, 2013**

Onthomastax coprinus: Rasnitsyn and Aristov, 2013, p. 605, text-fig. 14b, 15g.

Holotype. PIN, no. 3286/146, part and counterpart imprints of an incomplete and somewhat squashed forewing in a fish coprolite; Russia, Udmurtia, Zavialovsky District, Rassokha River near the village of Chepanikha; Middle Permian, Urzhumian Stage.

Description (Fig. 2k). See genus diagnosis.

Measurements in mm: wing fragment length 11.3; width 4.3; apparent complete length of the wing 13.

Material. Holotype.

Genus *Palaeomantopsis* Martynov, 1928

Palaeomantopsis: Martynov, 1928, p. 83; Carpenter, 1992, p. 133; Aristov and Rasnitsyn, 2023a, p. 74.

Type species. *Palaeomantopsis furcatella* Martynov, 1928.

Diagnosis. Forewing with four-branched RS. Forks of M and CuA near or distal to the base of RS.

Species composition. Type species and *Palaeomantopsis nana* (Storozhenko, 1992) from the Middle and Late Permian of Russia and Mongolia.

Comparison. See key for the genera.

Remarks. The genus was described as *Miomoptera incertae sedis* (Martynov, 1928), later assigned to Protorthoptera family uncertain (Carpenter, 1992) and later assigned to Permosialidae as a separate genus (Aristov and Rasnitsyn, 2023a). These specimens are not considered as aberrations of the *Permosialis* with an additional fork of RS because both these genera are too much different from the comparable species from the studied localities and are unlikely to represent their aberrant forms. *P. furcatella* is distinguished from *P. paucinervis* in an almost straight stem of RS (strongly curved in *P. paucinervis*), in *P. nana*, R is distinctly weakened in the distal third (in *P. postuma*, it is distinct almost to the apex).

***Palaeomantopsis furcatella* Martynov, 1928**

Palaeomantopsis furcatella: Martynov, 1928, p. 83, pl. 11, fig. 4; Aristov and Rasnitsyn, 2023a, p. 74, text-figs. 2e–2z, pl. 9, figs. 6–8.

Permosialis quadriramosa: Martynova, 1952, p. 229, text-fig. 24; Aristov and Rasnitsyn, 2023a, p. 74 (as of *P. furcatella* Martynov, 1928).

Holotype. PIN, no. 2065/23(32), part and counterpart imprints forewing; Russia, Tatarstan, right bank of the Kama River near the Tikhie Gory pier, Tikhie Gory locality; Middle Permian, Kazanian Stage, Lower Kazanian Substage, Baitugan Formation, *Lingula* Beds.

Description (Figs. 2l, 2m). The anterior margin of the forewing weakly convex. Branches of SC are similar in length to the distance between them. R with short fork; RS begins in the basal quarter of the wing. The stem of RS is almost half the length of RS, forks of RS lie at approximately equal distances, the last fork is very short. The first fork of RS slightly distal to the forks of M and CuA, located on the same level near the mid-wing. M_5 is present. The fork of CuA is slightly narrower than the fork of M; branches of CuA and CuP are without a kink. In the hindwing, R is with a short fork. RS begins to branch much earlier than in the forewing, stem of RS_{1+2} and the fork of RS_{1+2} are much longer. The fork of M at the level of the second fork of RS. The fork of CuA is at the level of the first fork of RS. Coloring is missing or not preserved.

Measurements in mm: forewing length 12–15, hindwing length 11.

Comparison. Differs from *P. nana* in having shorter SC branches, a longer stem of RS and a short fork of RS_{1+2} .

Occurrence. Middle Permian (Lower Kazanian Substage); Russia, Arkhangelsk Region and Tatarstan.

Material. Apart from the holotype, two imprints from the Ivagora Formation of the Soyana River, Arkhangelsk Region (Aristov and Rasnitsyn, 2023a).

***Palaeomantopsis nana* (Storozhenko, 1992)**

Tologoptera nana: Storozhenko, 1992, p. 126, text-figs. 5a–5v, pl. 32, fig. 3.

Palaeomantopsis nana: Aristov and Rasnitsyn, 2023b, p. 71, text-figs. 2e–2z, pl. 11, figs. 6, 7.

Holotype. PIN, no. 4305/319, part and counterpart imprints of an incomplete forewing; Mongolia, South Gobi aimag, Bor-Tologoi locality; Upper Permian, Wuchiapingian Stage, Tsankhin Formation.

Description (Fig. 2n). The anterior margin of the forewing is convex. The anterior branches of SC are almost twice the distance between them. R is simple, in the distal third very weak. R has a short fork. RS begins in the basal quarter of the wing. Forks of RS, M and CuA are approximately at the same level before the mid-wing. The stem of RS is no more than a third of the length of RS, the last fork is long (not shorter of

its stem). M_5 is present. Branches of CuA and CuP without a kink. The fork of CuA is not narrower than the M fork at the base. Coloration is either absent or not preserved.

Measurements in mm: forewing length 13.6–16.9, width 7.1–7.5

Comparison. Differs from *P. furcatella* in longer branches of SC, shorter RS stem and long fork RS_{1+2} .

Material. Holotype and two paratypes from the type locality (Aristov and Rasnitsyn, 2023b).

ACKNOWLEDGMENTS

The authors are grateful to S.Yu. Storozhenko (FSC Biodiversity Far East Branch, Russian Academy of Sciences) and V.D. Ivanov (St. Petersburg State University) for constructive criticism of previous versions of the work and important recommendations.

FUNDING

The study was supported by the Russian Science Foundation, project no. 21-14-00284.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

- Aristov, D.S., Classification of order Eoblattida (Insecta; Blattodea) with description of new taxa, *Far Eastern Entomol.*, 2015, no. 301, pp. 1–56.
- Aristov, D.S. and Rasnitsyn, A.P., Position and taxonomy of the Permian fossil insect family Permobiidae (Insecta: Palaeomanteida = Miomoptera), *Russ. Entomol. J.*, 2008, vol. 17, pp. 327–334.
- Aristov, D.S. and Rasnitsyn, A.P., New and little-known species of the genus *Permosialis* (Insecta: Palaeomanteida: Permosialidae) from the Middle Permian of Russia, *Far Eastern Entomol.*, 2022, no. 467, pp. 17–22.
- Aristov, D.S. and Rasnitsyn, A.P., Revision of Permosialidae (Insecta: Palaeomanteida) from the Uppermost Lower and Lower Middle Permian of European Russia, *Paleontol. J.*, 2023a, vol. 57, no. 2, pp. 187–196.
- Aristov, D.S. and Rasnitsyn, A.P., New and Little Known Permosialidae (Insecta: Palaeomanteida) from the Upper Permian of Mongolia and the Middle or Upper Triassic of Kyrgyzstan, *Paleontol. J.*, 2023b, vol. 57, no. 4, pp. 422–431.
- Aristov, D.S., Rasnitsyn, A.P., and Naugolnykh, S.V., New Blattiniopsidae (Insecta: Blattiniopsida) in the Permian of the Pechora Basin (Komi Republic, Russia) in the context

of landscape and vegetation evolution, *Paleontol. J.*, 2021, vol. 55, no. 6, pp. 641–649.

Carpenter, F.M., The Lower Permian insects of Kansas: Part 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plecoptera and Protoperlaria, *Proc. Amer. Acad. Arts Sci.*, 1939, vol. 73, pp. 29–70.

Carpenter, F.M., Superclass Hexapoda, in *Treatise on Invertebrate Paleontology, Part R: Arthropoda 4*, vols. 3–4. Boulder, Colorado: Geol. Soc. Amer., Univ. Kansas Press, 1992.

Güthorl, P., Zur Arthropoden-Fauna des Karbons und Perms. 9. Palaeodictyoptera, Mixotermioidea, Miomoptera und Blattariae, *Senckenbergiana*, 1939, vol. 21, pp. 314–329.

Hong, Y.-C. and Guo, X.-R. Two new Middle Triassic genera and species of Mesopanorpididae from Shaanxi (Insecta, Mecoptera), *Acta Zootaxonomica Sin.*, 2003, vol. 28, pp. 716–720.

Kukalová, J., Permian insect of Moravia. Part I. Miomoptera, *Sb. Geol. Ved.*, 1963, vol. 1, pp. 7–52.

Martynov, A.V., Über eine neue Ordnung der fossilen Insekten *Miomoptera* nov., *Zool. Anz.*, 1927, vol. 72, pp. 99–109.

Martynov, A.V., Permian fossil insects of North-East Europe, *Tr. Geol. Muzeya Akad. Nauk SSSR*, 1928, vol. 4, pp. 1–118.

Martynov, A.V., Permian fossil insects of the Arkhangelsk Region. Part II. Neuroptera, Megaloptera and Coleoptera, with a description of two new beetles from Tikhie Gory, *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 1933, vol. 2, pp. 63–96.

Martynov, A.V., Lias insects of Shurab and Kyzyl-Kiya, *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 1937, vol. 7, no. 1, pp. 1–231.

Martynova, O.M., Permian Neuroptera of the USSR, *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 1952, vol. 40, pp. 197–237.

Martynova, O.M., Order Megaloptera, *Trudy Paleontol. Institute Akad. Nauk SSSR*, 1961, vol. 85 (Rodendorf, B.B., Bekker-Migdisova, E.E., Martynova, O.M., and Sharov, A.G. Paleozoic insects of the Kuznetsk Basin), pp. 469–473.

Martynova, O.M., Order Megaloptera, in *Osnovy Paleontologii, vyp. 9 Chlenistonogie – trakheynye i khelitserovye* (Fundamentals of Paleontology, Vol. 9. Arthropods. Arthropoda, Tracheata, Chelicerata), Rodendorf, B.B., Ed., Moscow: Akad. Nauk SSSR, 1962, pp. 269–270.

Novokshonov, V.G. and Rasnitsyn, A.P., A new species of insects of the order Palaeomanteida = Miomoptera from the Lower Permian of Chekarda (Perm Region), *Vestn. Perm. Univ. Ser. Geol.*, 2001, no. 3, pp. 110–114.

Novokshonov, V.G. and Zhuzhgov, L.V., 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, *Paleontol. J.*, 2004, vol. 38, Suppl. 2, pp. 173–184.

Prokop, J., Pecharová, M., Garrouste, R., et al., Redefining the extinct orders Miomoptera and Hypoperlida as stem acercarian insects, *BMC Evol. Biol.*, 2017, vol. 17:205, pp. 1–20.

<https://doi.org/10.1186/s12862-017-1039-3>

- Rasnitsyn, A.P., New Paleozoic and Mesozoic insects, *Paleontol. Zh.*, 1977, no. 1, pp. 64–77.
- Rasnitsyn, A.P., The origin and evolution of Hymenoptera, *Tr. Paleontol. Inst. Akad. Nauk SSSR*, 1980a, vol. 174, pp. 1–192.
- Rasnitsyn, A.P., Order Palaeomanteida Handlirsh, 1906, in *Tr. Paleontol. Inst. Akad. Nauk SSSR*, vyp. 175 (Trans. Paleontol. Inst. USSR Acad. Sci. Historical Development of the Class of Insects, Vol. 175, Rodendorf, B.B. and Rasnitsyn, A.P., Eds., 1980b).
- Rasnitsyn, A.P., Order Palaeomanteida Handlirsch, 1906, in *History of Insects*, Rasnitsyn A.P. and Quicke, D.L.J., Eds., Dordrecht: Kluwer Acad. Publ., 2002, pp. 161–164.
- Rasnitsyn, A.P. and Aristov, D.S., New fossil insects (Insecta: Caloneurida, Hypoperlida, Palaeomanteida, Jurinida) from the Middle and Upper Permian of European Russia, *Paleontol. J.*, 2013, vol. 47, no. 7, pp. 678–704.
- Riek, E.F., Undescribed fossil insects from the Upper Permian of Belmont, New South Wales (with an appendix listing the described species), *Rec. Austral. Mus.*, 1968, vol. 27, no. 15, pp. 303–310.
- Riek, E.F., Upper Permian Insects from Natal, South Africa, *Ann. Natal Mus.*, 1976, vol. 22, pp. 755–789.
- Storozhenko, S.Yu., Grylloblattid insects of the Upper Permian of Eastern Kazakhstan, *Paleontol. Zh.*, 1991, no. 2, pp. 110–114.
- Storozhenko, S.Yu., New Mesozoic Grylloblattid insects (Grylloblattida) from Central Asia, *Paleontol. Zh.*, 1992a, no. 1, pp. 67–75.
- Storozhenko, S.Yu., *New fossil Grylloblattid insects (Insecta: Grylloblattida) from Mongolia*, in *Novye taksony iskopyayemykh bespozvonochnykh Mongolii. Tr. Sovm. Ross.-Mongol. Paleontol. Eksped.*, vyp. 41 (New Taxa of Fossil Invertebrates from Mongolia. Trans. Joint Russ.-Mongol. Paleontol. Exped., Vol. 41), Grunt, T.A., Luvsandanzan, B., and Tatarinov, L.P., Eds., Moscow: Nauka, 1992b, pp. 122–129.
- Storozhenko, S.Yu. and Novokshonov, V.G., To the knowledge of the fossil family Permosialidae (Insecta: Miomoptera), *Far Eastern Entomol.*, 1999, no. 76, pp. 1–5.
- Tillyard, R.J., Kansas Permian insects. Part 12. The family Delopteridae, with a discussion of its ordinal position, *Am. J. Sci.*, 1928, vol. 16, pp. 469–484.
- Tillyard, R.J., Kansas Permian insects. Part 17. The order Megasecoptera and additional to the Palaeodictyoptera, Odonata, Protoperlaria, Copeognatha and Neuroptera, *Amer. J. Sci.*, 1937, vol. 33, pp. 81–110.

Translated by S. Nikolaeva

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