

New and Little Known Permosialidae (Insecta: Palaeomanteida) from the Upper Permian of Mongolia and the Middle or Upper Triassic of Kyrgyzstan

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Abstract—The composition of the family Permosialidae (Insecta: Palaeomanteida) from the Upper Permian deposits of Mongolia and Kazakhstan is revised. *Permosialis postuma* sp. nov. and *P. virgata* sp. nov. are described and *P. mongolica* (Storozhenko, 1992) comb. nov. (= *Tologoptera mongolica* Storozhenko, 1992) and *Palaeomantopsis nana* (Storozhenko, 1992) comb. nov. (= *Tologoptera nana* Storozhenko, 1992) are redescribed from the Wuchiapingian Bor-Tologoy fossil insect site in South Gobi Aimag, Mongolia. *Permosialis frivulus* (Storozhenko, 1991) is redescribed from the Changhsingian Karaungir locality in East Kazakhstan Region of Kazakhstan. *P. triassica* Novokshonov et Zhuzhgo is redescribed from the Ladinian or Carnian Dzhaliloucho (Madygen) Lagerstätte in Kyrgyzstan. A new synonymy is established: *Permosialis asiatica* Martynova, 1961 = *P. sibirica* Martynova, 1961, syn. nov.

Keywords: fossil insects, Ak-Kolka Formation, Maichat Formation, Madygen Formation, Tsanhin Formation

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INTRODUCTION

The Bor-Tologoy fossil insect site is located in the South Gobi aimag of Mongolia and belongs to the Tsanhin Formation of the Wuchiapingian Stage (according to <http://www.fossilworks.org/>) of the Upper Permian (“? Severodvinian Stage”: Shcherbakov, 2008). The first Palaeomanteida from Bor Tologoy were described as two new species of a new genus (*Tologoptera mongolica* Storozhenko, 1992; *T. nana* Storozhenko, 1992) within the new family Tologopteridae assigned to the order Grylloblattida (Storozhenko, 1992). Subsequently, this family was synonymized under the Permosialidae of the order Palaeomanteida (Storozhenko and Novokshonov, 1999). This revision shows the presence in Bor-Tologoy of two genera and four species of Permosialidae: *Permosialis mongolica* (Storozhenko, 1992), *P. postuma* sp. nov., and *P. virgata* sp. nov. and *Palaeomantopsis nana* (Storozhenko, 1992). Permosialidae make up about 5% of the remains in Bor-Tologoi, which makes the Permosialidae fauna of this locality the richest and most diverse of all Late Permian fossil insect faunas, despite the fact that due to insufficient preservation, most of the Permosialidae material from here (32 specimens out of 51) cannot be identified beyond family level. The

material from Kazakhstan comes from the East Kazakhstan region, the Saur Ridge, the right bank of the Karaungir River at the mouth of Maychat and Ak-Kolka creeks; Upper Permian, Changhsingian/Vyatkian Stage, Maichat and Ak-Kolka formations. About 550 insect remains were collected here (Aristov et al., 2013, p. 796), of which 30 (5.5%) were assigned to Permosialidae. Most of the latter are small fragments of wings, therefore, as in Bor-Tologoy, more or less confidently identifiable remains are in the minority. Based on this material, Storozhenko (1991) described *Sarbalopterodes frivulus* Storozhenko, 1991 in the order Grylloblattidae. Later, the genus was transferred to Permosialidae (Storozhenko and Novokshonov, 1999), and the species was assigned to the genus *Permosialis* (Rasnitsyn and Aristov, 2013). Thus, the fauna of Karaungir is also unusually rich in permosialids, although they are not very diverse (one identified species). In other Upper Permian localities, permosialids are scarce. They are described from the Severodvinian (Wuchiapingian) Isady locality in Russia and from the Changhsingian in Belmont, NSW, Australia. In Isady, Permosialidae are represented by a single species, *Epi-mastax mutovinensis* Rasnitsyn et Aristov, 2013 (Rasnitsyn and Aristov, 2013), and in Belmont, by a single species, *Permosialis belmontensis* Riek, 1968 (Riek, 1968). In these two localities, permosialids make up

[†] Deceased.

less than one percent of all insect fossils found. The reasons for the similarity between the Bor Tologoy and Karaungir faunas and their differences from other Late Permian faunas require special analysis. The Dzhaloucho site is located in the Dzhaloucho Stow in the Batken District of the Osh Region, Kyrgyzstan. Its insect-bearing deposits belong to the Madygen Formation assigned to the Ladinian or Carnian Stage of the Middle or Late Triassic, respectively (Shcherbakov, 2008; Voigt et al., 2017). About 25000 insect remains have been collected here (Voigt et al., 2017), of which only four have been identified as Permosialidae. This is the only Triassic locality where Permosialidae are found.

MATERIAL

The material described in this work is housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS).

SYSTEMATIC PALEONTOLOGY

Order Palaeomanteida

Family Permosialidae Bolton, 1925

Genus *Permosialis* Martynov, 1928

Permosialis mongolica (Storozhenko, 1992)

Plate 10, figs. 1–4

Tolgoptera mongolica: Storozhenko, 1992, p. 126, text-figs. 4a–4e; pl. 32, fig. 2; Storozhenko, Novokshonov, 1999, p. 4, text-fig. 2.

Permosialis mongolica: Rasnitsyn and Aristov, 2013, p. 691.

Holotype. PIN, no. 4305/286, part and counterpart imprints of an incomplete forewing; Mongolia, South Gobi aimag, 16 km SE of Tsogttsetsii somon, Bor-Tologoy Stow, 20 km East-North-East from Tabun-Tologoy Quarry, Bor-Tologoy locality; Upper Permian, Wuchiapingian Stage, Tsanhin Formation.

Description (Figs. 1a–1d). Coloration is absent on most of the remains; occasionally broad transverse stripes are visible across the entire wing (up to five or six, pl. 10, fig. 3); sometimes a darker spot is formed on the pre-apical stripe (pl. 10, fig. 4).

The anterior margin of the forewing is convex, the costal area is wide. SC is slightly curved, its anterior branches long (several times longer than the distance between them in the middle part). R is slightly S-curved, weak in distal third, often barely visible. The RS and M bifurcations are more or less at the same level, the CuA bifurcation is usually slightly more distal. The branches of RS and M are clearly bent backwards. The stem of RS_{1+2} is a fraction of the length of the RS stem, the RS_{1+2} fork is before the mid-wing. M_5 is present. The stem and branches of CuA are concave. The intercubital field has two rows of cells. The hindwing is not reliably known (one almost complete and two relatively large fragments of the hindwing of *Permosialis* were found in the locality, but they are too

small, about 12–13 mm long, and, unlike the forewing of *P. mongolica*, have a relatively very long stem of RS_{1+2}).

Measurements in mm: length of forewing of holotype 26.5, width 11.3; paratype no. 4305/298: length 25.2, width 11.8; other wings are fragmentary. Aberrant specimen no. 4305/322: fragment length 18.6, width 12.6, probable total wing length 21–22.

Comparison. The new species is very similar to *P. asiatica* Martynova, 1961 (= *P. sibirica* Martynova, 1961, syn. nov.) with a very short stem RS_{1+2} (a fraction of the length of the RS stem), as well as in the veins of the distal part of the wing bent backward (including RS_1), but differs from it by R, sharply weakened in its distal third and in the presence of M_5 (in *P. asiatica*, R is convex and distinct almost to the apex; M and CuA are merged in a short space; M_5 is absent).

Remarks. The vast majority of the remains are incomplete, so their identification is provisional, and the description and measurements are based on the few best-preserved specimens. Among the latter specimens, there is a shortened wing (Fig. 1d; Pl. 10, fig. 4): about 1.6–1.7 times as long as wide (2.4 times in the holotype). At the same time, no significant differences in venation are observed, but a small dark spot is noticeable in the anterior part of the distal quarter of the shortened wing, which is absent in other specimens. It seems to us that this is rather a subbrachypterous form of the same species, rather than a different species. Synonymization of *P. asiatica* Martynova, 1961 (= *P. sibirica* Martynova, 1961, syn. nov.) is related to the statement of Martynova (1961) on the presence of a short crossvein connecting M and CuA. It is based on the erroneous identification of the wing deformation as the base of CuA, which is actually noticeably smoothed and located basal to the M + CuA fork. Other differences between *P. sibirica* and *P. asiatica* cited in the description rather correspond to intraspecific variability.

Material. In addition to the holotype, paratypes PIN, nos. 4305/287, 289, 292, 293, 296, 298, 303, 304, 306, 307, 314, 322, 325, 327, 337, 338, 341, 359, as well as those specimens not included in the type series PIN, nos. 4305/272, 349 from the same locality.

Permosialis postuma Aristov et Rasnitsyn, sp. nov.

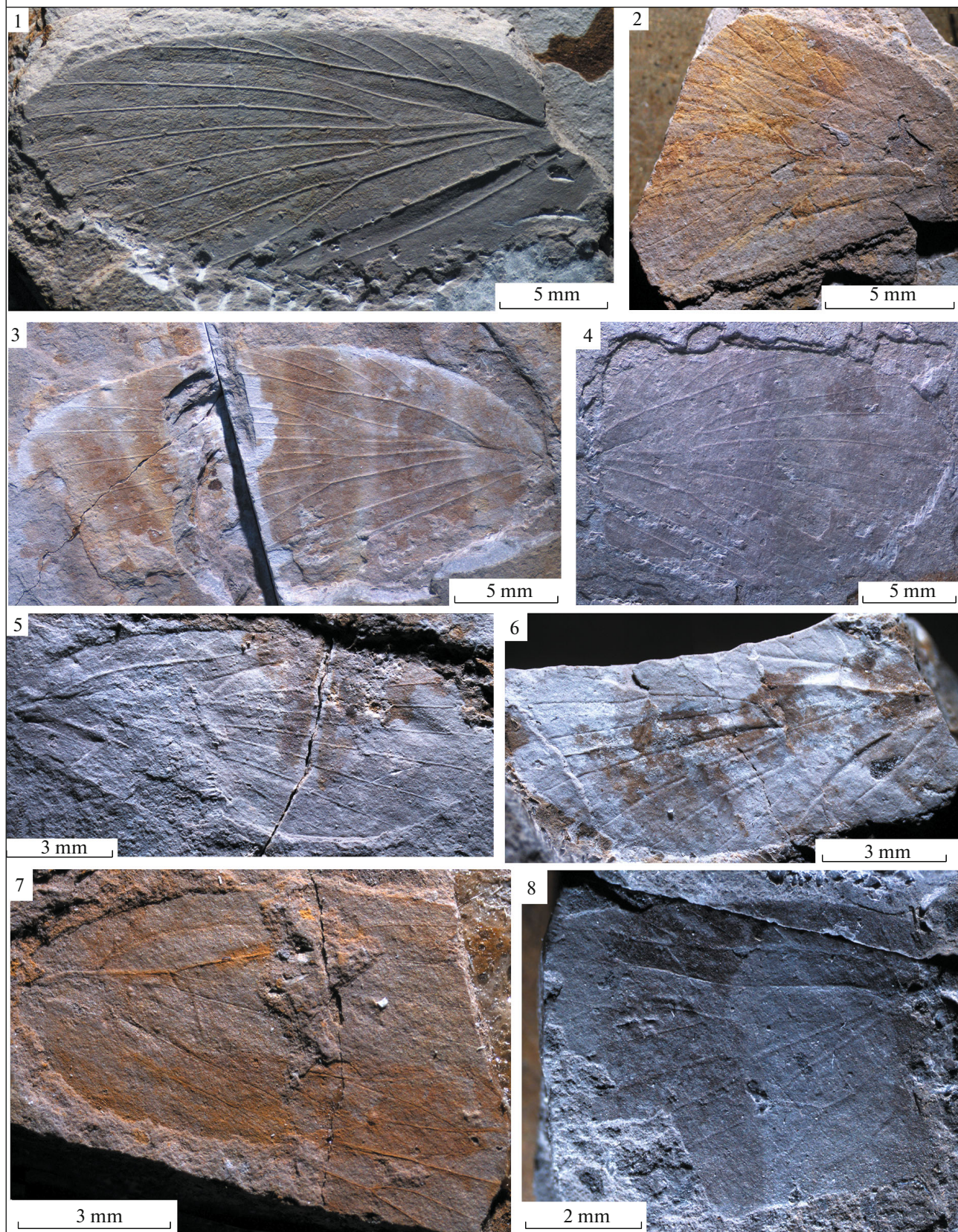
Plate 10, figs. 5–7

Tolgoptera nana: Storozhenko, 1992 (pars, only paratype no. 4305/321).

Etyymology. From the Latin *postumus* (last, the most junior).

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

Description (Figs. 1e–1g). No coloration is preserved. The anterior margin of the forewing con-



vex, costal area is moderately wide. SC is slightly curved; its anterior branches are not long (less than twice as long as the distance between them). R is slightly S-curved, distinct up to (or almost up to) apex. Forks RS, M and CuA are more or less at the same level. The stem of the RS is almost straight, the first fork of the RS is before the mid-wing; the RS_{1+2} stem is slightly shorter than the RS stem. M_5 is developed. The stem and branches of CuA are concave. The hindwing is not known.

Measurements in mm: holotype forewing length is 14.6, width is 5.9, paratype forewing length no. 4305/401 is 11.4, width on the imprint is 5.9, total width is probably 6.0.

Comparison. The new species is most similar to *P. paucivena* in relatively short SC branches, not shortened stem RS_{1+2} , broad wing tip, and absence of regular spots, but differs in the more basal position of the first fork of RS and an almost straight stem of RS.

Material. In addition to the holotype, paratypes PIN, nos. 4305/379, 401.

Permosialis virgata Aristov et Rasnitsyn, sp. nov

Plate 10, fig. 8

Tolgoptera mongolica: Storozhenko, 1992 (pars, only paratype no. 4305/279).

Etymology. From the Latin *virgatus* (striped).

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

Description (Fig. 1h). Judging from the surviving fragment, the fore wing has a darkened base, anterior margin, and a transverse stripe through the stem of RS_{1+2} and further through the basal half of the M fork and the CuA fork. The anterior margin of the wing is convex; SC almost straight in the visible part, with short branches. R distally (from the level of the fork RS_{1+2}) is weak and concave. The RS, M and CuA forks are at the same level. The RS and RS_{1+2} stems are curved, the RS_{1+2} stem is longer than half of the RS stem. In the intercubital field, a strong oblique cross-vein directed to the fork of CuA, CuP is broken at the place where it begins. The hindwing is unknown.

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

Comparison. This species differs from other species of *Permosialis* in the coloration of the wing with darkening, leaving a large light spot opening backwards in at the mid-wing and a light (possibly not entirely) apex of the wing, and in the venation, i.e., in the presence of a prominent oblique cross-vein in the intercubital field. Otherwise, the new species is similar in venation to *P. paucinervis*, except for the weakened distal part of R.

Material. Holotype.

Permosialis frivola (Storozhenko, 1991)

Plate 11, figs. 1–5

Sarbalopterodes frivulus: Storozhenko, 1991, p. 112

Permosialis frivola: Rasnitsyn and Aristov, 2013, p. 691.

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

Description (Figs. 2a–2f, 3). The coloration is often bright (not preserved on many imprints, including the holotype) and extremely variable. The most characteristic are large, rimmed spots (Fig. 3a, 3c, 3d), darkening along the crossveins (Fig. 3b) or vice versa, light crossveins on a dark background (Pl. 11, fig. 5); sometimes a separate bright spot on an unpainted wing, showing that it is not always a matter of secondary colour loss. The anterior margin of the forewing within the SC (except for the very base) is almost straight, the costal area is comparatively narrow. SC almost straight, its anterior branches only slightly longer than the distance between them. R is almost straight, distinct almost up to the apex. Forks RS, M and CuA are more or less on the same level. At least the branches of RS_1 and RS_2 are not bent backwards. Stem RS_{1+2} is 0.67 the length of stem RS, fork RS_{1+2} is behind the mid-wing. M and CuA are merged in a short segment (M_5 is not present). The stem and branches of CuA are concave. The intercubital field has two rows of cells. The hindwing (Figs. 2d, 2f) with the same shortened stem RS_{1+2} as in the anterior wing, but the M fork is shifted distally relative to the RS and CuA forks, and the M stem is with a kink at the entry of a cross-vein, which originates from the first R fork.

Measurements in mm: length of forewing of specimen PIN no. 2781/24(1) 21.6, width 10.8

Explanation of Plate 10

Figs. 1–4. *Permosialis mongolica* (Storozhenko, 1992), forewings: (1) holotype PIN, no. 4305/286; (2) paratype PIN, no. 4305/314; (3) paratype PIN, no. 4305/298; (4) paratype PIN, no. 4305/322.

Figs. 5–7. *Permosialis postuma* sp. nov., forewings: (5) holotype PIN, no. 4305/321; (6) paratype PIN, no. 4305/401; (7) paratype PIN, no. 4305/379.

Fig. 8. *Permosialis virgata* sp. nov., holotype PIN, no. 4305/279, forewing.

Mongolia, South Gobi aimag, Bor-Tologoy locality; Upper Permian, Wuchiapingian Stage, Tsanhin Formation.

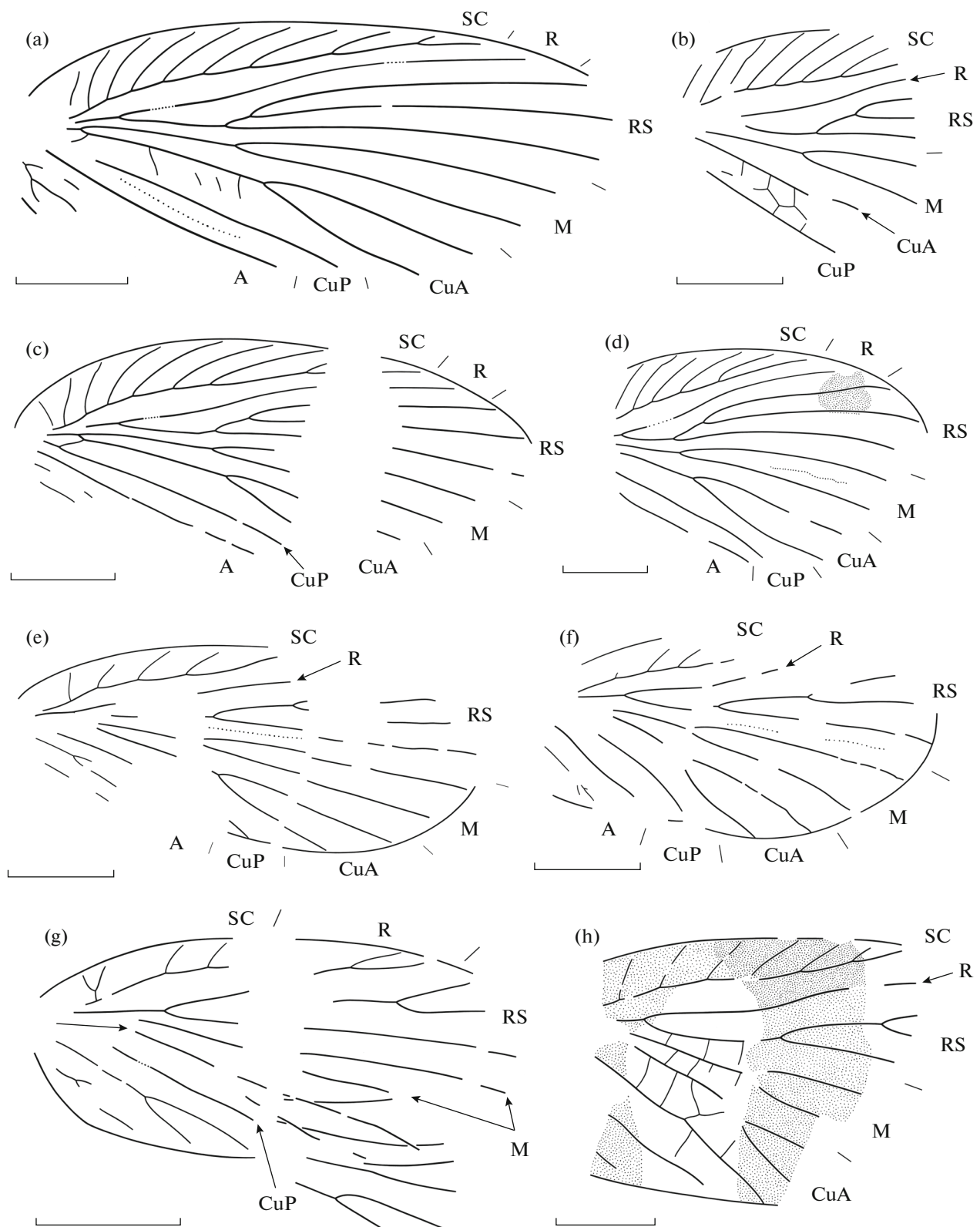


Fig. 1. Members of the family Permosialidae from the Upper Permian of Mongolia, forewings: (a–d) *Permosialis mongolica* (Storozhenko, 1992): (a) holotype PIN, no. 4305/286, (b) paratype PIN, no. 4305/314, (c) paratype PIN, no. 4305/298, (d) paratype PIN, no. 4305/322; (e–g) *Permosialis postuma* sp. nov.: (e) holotype PIN, no. 4305/321, (f) paratype PIN, no. 4305/401, (g) paratype PIN, no. 4305/379; (h) *P. virgata* sp. nov., holotype PIN, no. 4305/279. Scale bar (a–d) 5, (e–g) 3, (h) 2 mm.

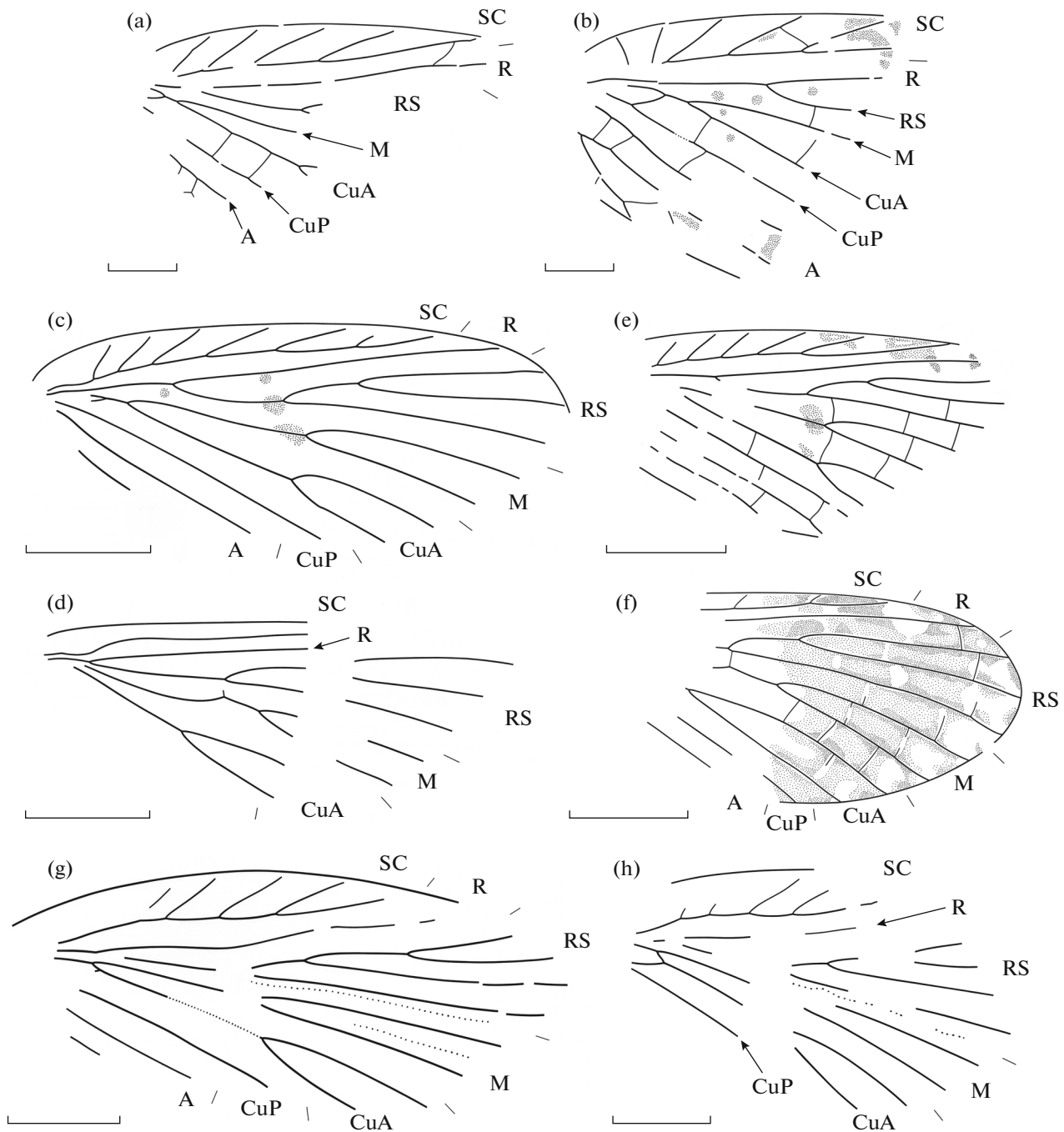


Fig. 2. Representatives of the family Permosialidae from Upper Permian of Kazakhstan: (a–f) and Mongolia (g, h): (a–f) *Permosialis frivola* (Storozhenko, 1991): (a) holotype PIN, no. 2494/31, (b) specimen PIN, no. 2781/168, forewings; (c, d) PIN, no. 2781/241: (c) reconstruction of a forewing, (d) reconstruction of hindwings; (e) specimen PIN, no. 2781/243, forewing; (f) specimen PIN, no. 2781/137, hindwing; (g, h) *Palaeomantopsis nana* (Storozhenko, 1992), forewings: (g) holotype PIN, no. 4305/319, (h) paratype PIN, no. 4305/344. Scale bar (a, b) 2, (c–f) 5, (g, h) 2 mm.

(other remains are too fragmentary for measurements).

Comparison. The species differs from other species in the anterior margin of the forewing, which is almost straight almost from the base (in *P. belmontensis*, the anterior margin is straight in a smaller seg-

ment) and often with unusual coloration (large, rimmed spots, see description). Differs from all species, except for *P. asiatica*, by the merging of M and CuA in a short segment. Differs from *P. asiatica* in narrow costal area with short SC branches (in *P. asiatica*, SC branches are long). It additionally differs from



Fig. 3. *Permosialis frivola* (Storozhenko, 1991) from the Upper Permian of Mongolia, variants of coloration: (a) specimen PIN, no. 2781/153; (b) specimen PIN, no. 2781/222; (c) specimen PIN, no. 2781/182; (d) specimen PIN, no. 2781/184. Scale bar (a, c) 2, (b, d) 1 mm.

P. belmontensis in the position of the RS fork near the mid-wing (in *P. belmontensis*, the RS branches in the distal third of the wing).

Material. In addition to the holotype, paratypes PIN, nos. 2781/151, 153, 158, 164, 166*, 173, 174, 180, 181*, 182, 183, 184, 186, 187*, 189*, 190*, 194, 196*, 198*, 199, 222, 239, 240, 241**, 242, 243, 250*, 259* (one asterisk marks the imprints of the hind wings, two asterisks indicate a specimen with four wings).

***Permosialis triassica* Novokshonov et Zhuzhgova, 2004**

Permosialis triassica: Novokshonov and Zhuzhgova, 2004, p. S183.

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

Description (Fig. 4). Coloration not preserved. The anterior margin of the forewing is slightly convex, the costal area is comparatively narrow. SC is almost straight. R is almost straight, sharp almost to

the apex. Forks RS, M and CuA more or less at the same level within the first quarter of the wing, all their distal branches are bent backwards. Stem RS_{1+2} is much longer than stem RS. Fork RS_{1+2} is before the mid-wing. The trunk and branches of CuA are concave. Hind wing with forks RS, M, and CuA, also shifted basally to the border of the first third of the wing. The stem of RS_{1+2} is longer than in the front wing. The RS, M, and CuA branches are distally curved backwards. The stem of RS_{1+2} is longer than in the front wing. The RS, M, and CuA branches are distally curved backwards.

Measurements in mm: The incomplete forewing of the holotype is 14.7 long and 7.1 wide.

Comparison. It differs from other species in the basal position of the forks RS, M, and CuA (within the first quarter of the forewing).

Material. Apart from the holotype, hindwings PIN, nos. 2069/3592, 2555/743, 2067, 2068, 2785/3343, 5330/117.

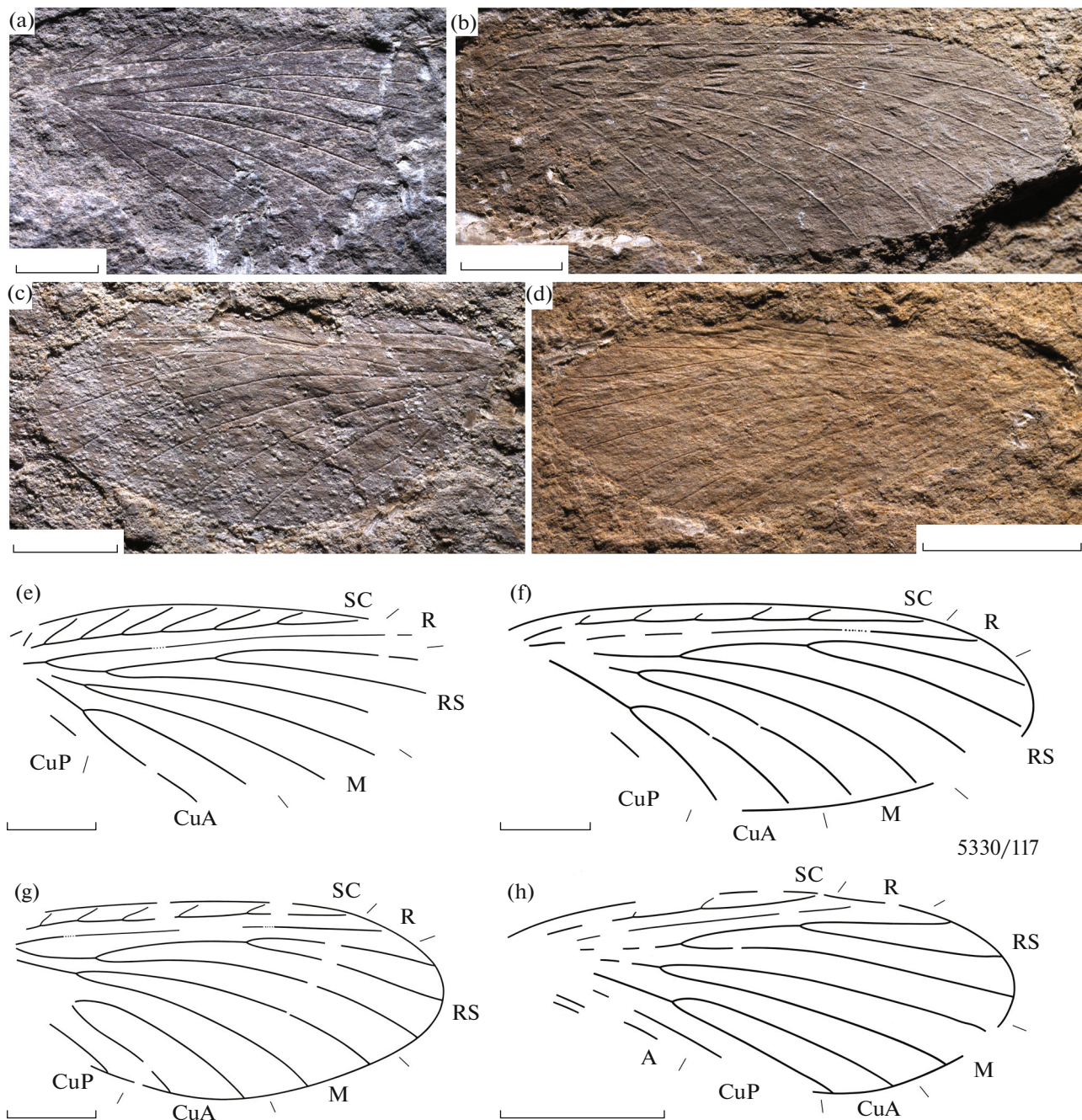


Fig. 4. *Permosialis triassica* Novokshonov et Zuzhgova, 2004 from the Middle–Upper Triassic of Kyrgyzstan, photograph and interpretation: (a, e) holotype PIN, no. 2555/2066, forewing; (b, f) specimen PIN, no. 2785/3343, hindwing; (c, g) specimen PIN, no. 2555/743, hindwing; (d, h) specimen PIN, no. 5330/117, hindwing. Scale bar 3 mm.

Genus *Palaeomantopsis* Martynov, 1928

Palaeomantopsis nana (Storozhenko, 1992), comb. nov.

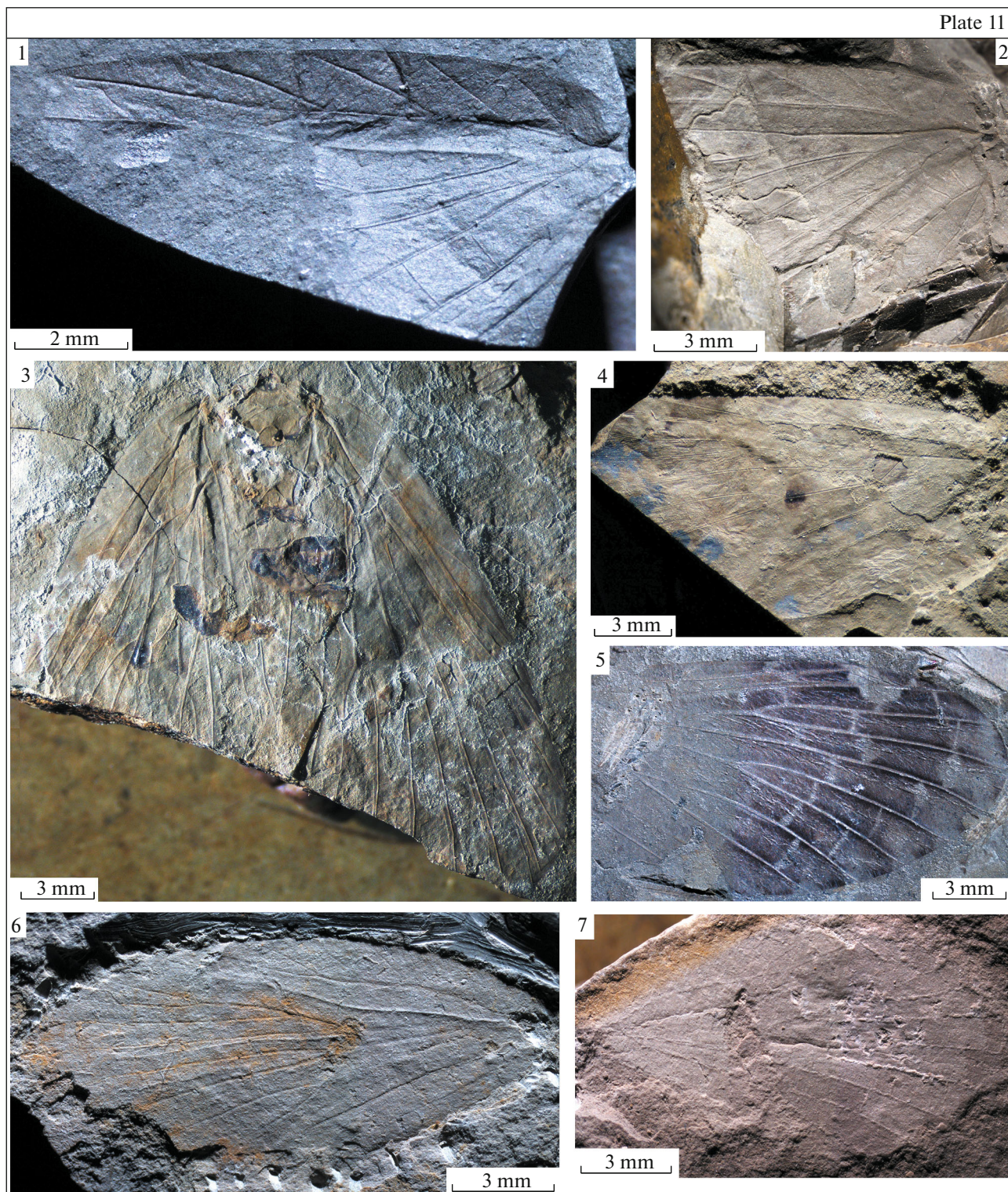
Plate 11, figs. 6–7

Toloptera nana: Storozhenko, 1992, p. 126, text-figs. 5a–5c; pl. 32, fig. 3.

Holotype. PIN, no. 4305/319, part and counterpart imprints of an incomplete forewing; Mongolia,

South Gobi aimag, Bor-Tologoy locality; Upper Permian, Wuchiapingian Stage, Tsanhin Formation.

Description (Figs. 2g, 2h). Coloration is either absent or not preserved. The anterior margin of the forewing is convex; the costal field is wide. SC is weakly S-curved, its anterior branches are not long (less than twice as long as the distance between them). R is weakly S-curved, very weak in the distal third.



Explanation of Plate 11

Figs. 1–5. *Permosialis frivola* (Storozhenko, 1992): (1, 2) forewings: (1) holotype PIN, no. 2494/31, (2) paratype PIN, no. 2781/168; (3, 4) paratype PIN, no. 2781/241: (3) forewing and (4) hindwing; (5) specimen PIN, no. 2781/243, forewing.

Figs. 6, 7. *Palaeomantopsis nana* (Storozhenko, 1992): (6) holotype PIN, no. 4305/319, forewing; (7) paratype PIN, no. 4305/344, forewing.

(1–5) Kazakhstan, East Kazakhstan region, locality Karaungir; Upper Permian, Changhsingian Stage, (1) Maichat Formation, (2–5) Ak-Kolka Formation; (6, 7) Mongolia, East Gobi aimag, Bor-Tologoy locality; Upper Permian, Wuchiapingian Stage, Tsanhin Formation.

Forks RS, M and CuA are more or less at the same level. Branches of RS not curved or only slightly curved backwards. RS 4-branched, the first fork of RS is before the mid-wing, RS₁₊₂ is long. M₅ is present. The stem and branches of CuA are concave. Hindwings are not known.

Measurements in mm: holotype: length of forewing 16.9, width 7.1; in paratype no. 4305/344 13.6 and 7.5, respectively.

Comparison. Differs from *P. furcatella* Martynov, 1928 sensu Aristov and Rasnitsyn (2023) in the position of the first RS fork before the mid-wing and a weak RS in its distal part.

Remarks. As after the transfer of *Tologoptera nana* to another family (Storozhenko and Novokshonov, 1999), the interpretation of the characters of this species had to be emended, four-branched RS is now considered as not an aberration, but as a character of a different genus. Consequently, many paratypes were not conspecific with the holotype. We consider some of them as incomplete wings of *Permosialis mongolica* (nos. 4305/267, 282, 357), some were included in the type series of *P. postuma* sp. nov. (nos. 4305/270, 321), and some remained unidentified.

Material. Apart from the holotype, paratypes PIN, nos. 4305/302, 344 from the same locality.

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CONFLICT OF INTERESTS

The authors claim that they have no conflict of interest.

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