

Most of the damage traces found in fossil plants (a considerable part of feeding traces and almost all galls) in the Isady locality are confined to oryctocoenoses with abundant fossils of complete leaves of the genus *Tatarina* and almost complete absence of fossil insects. In these deposits, up to 10% of leaves are damaged (70–80% of them are leaves with feeding traces and 20–30% have galls). Regular collecting in this locality has shown that, while the beds are relatively evenly filled with plant remains, the distribution of damaged leaves within the same bed and even the same surface is mosaic. This is primarily true of galls and, to a lesser extent, of feeding traces. Therefore, the above percentages are only approximate estimates. In the beds with insects, feeding and oviposition traces have been found. Fossil leaves in these beds are often strongly fragmented.

The confinement of injuries to leaves of *Tatarina* can be explained by both the greater attractiveness as food because of their thinner cuticle and smaller number of skeletal elements compared to conifers and the simple quantitative dominance of these remains in the oryctocoenoses.

To date, Isady remains the only large Upper Permian locality of insect-related damage or neoformations on plant leaves in Russia.

A rather poor assemblage of plant damage traces known from the Vyatkian deposits near the town of Vyazniki in the Vladimir Region (Sokovka and Baly-motikha localities) includes U-shaped structures on leaf blade margins and minelike formations rather similar in the type of tissue damage to *?Phagophytich-nus* sp. (Vasilenko, 2007, pl. 12, fig. 8). The interpretation of these formations remains difficult; some of them may actually prove to be mines. The interpretation of these damage traces as slits made by insects for building cocoons, proposed by Krassilov and Karasev (2008), is obviously inconsistent, taking into account the age of enclosing deposits. Note that similar structures have also been found on leaves of conifers in Triassic deposits of Ukraine and Jurassic–Cretaceous deposits of Transbaikalia (original unpublished data). The large prominent galls known from Sokovka (Krassilov and Karasev, 2009) are probably identical or very similar to *Paleogallus shcherbakovi*, described from Isady. In comparison with the ichnoassemblage from Normandien, the biodamage of plants found in Isady looks somewhat depleted and archaic due to the absence of leaf mines, lower morphological diversity of feeding traces, and presence of punctures in seeds, which are characteristic of more ancient assemblages.

Traces of plant–insect interaction found in Sokovka represent a mixed assemblage combining both Permian and Triassic forms.

2. SYSTEMATIC PALEONTOLOGY

2.1. New Fossil Insects (Insecta: Caloneurida, Hypoperlida, Palaeomanteida, Jurinida) from the Middle and Upper Permian of European Russia

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During the last decade, expeditions of the Arthropoda Laboratory of PIN collected rich materials on fossil insects of Middle and Upper Permian localities of Russia. The greatest amounts of material have been collected in the Urzhumian Chepanikha and Kostovaty localities, Udmurtia, the Severodvinian Novo-Aleksandrovka locality in the Orenburg Region and Isady, Vologda Region, and the Vyatkian Baly-motikha locality in Vladimir Region. These localities are discussed in detail in Chapter 1.

The new material enlarged considerably collections from these localities, the total number of insects in which was previously only a few dozen specimens. These collections have been partially treated, but the orders Caloneurida, Hypoperlida, Palaeomanteida, and Jurinida remained unexamined. The purpose of this study was to describe those materials. Members of the above orders are described from the Middle and Upper Permian of European Russia for the first time. The following new insect taxa are described below: from the Urzhumian Chepanikha locality, Udmurtia: Hypoperlida: *?Jarmilacladus patiens* sp. nov. (Ischnoneuridae), Palaeomanteida: *?Miomatoneurella rossoshana* sp. nov. (Palaeomanteidae), *Permosialis zavialovensis* sp. nov., *P. udmurtensis* sp. nov., *Epimastax tshepanikha* sp. nov., *Onthomastax coprinus* gen. et sp. nov. (Permosialidae), and Jurinida: *Eoglosselytrum biarmicum* sp. nov. and *?Isadelytron planum* sp. nov. (Jurinidae); from the Urzhumian Kargala locality, Orenburg Region: Hypoperlida: *Opisthocladus kargalensis* sp. nov. (Tococladidae); from the Urzhumian Kostovaty locality (Udmurtia): *Permosialis* sp. (Palaeomanteida: Permosialidae); from the Severodvinian Isady locality, Vologda Region: Caloneurida: *Isadistica issada* gen. et sp. nov., *Isadistica longa* sp. nov. (Caloneuridae), Hypoperlida: *Idelopsocus mutovinus* gen. et sp. nov. (Hypoperlidae), *Strephoptilus borealis* gen. et sp. nov., *S. longus* sp. nov. (Ischnoneuridae), Palaeomanteida: *?Trideloapterum indebitum* sp. nov. (Palaeomanteidae), *Epimastax mutovinensis* sp. nov. (Permosialidae), *Issapaloptera infracta* gen. et sp. nov., *Neembia ampla* gen. et sp. nov. (Permembidae), and Jurinida: *Isadelytron speciosum* gen. et sp. nov., *?Kara-jurina desperata* sp. nov. (Jurinidae); from the

Severodvinian Kul'chumovo locality, Orenburg Region: Jurinida: ?*Eoglosselytrum kultshumovense* sp. nov. (Jurinidae); from the Late Vyatkian Balymotikha locality, Vladimir Region: Palaeomanteida: *Balymotikha deterior* sp. nov. (Permosialidae). *Eohymen maculipennis* Martynov, 1937 (Caloneurida) is redescribed. The genera *Sarbalopterodes* Storozhenko, 1991 and *Tologoptera* Storozhenko, 1992 are synonymized under *Permosialis* Martynov, 1928. The genus *Epimastax* Martynov, 1928 is transferred to the family Permosialidae; the species *Glosselytrum martynovae* Ponomarenko 1988 and *G. linguale* Ponomarenko, 1988 are transferred to the genus *Mongoljurina* Ponomarenko, 1988 (comb. nov.). The families Anthracoptilidae Handlirsch, 1922 and Permarrhaphidae Martynov, 1931 are synonymized under Ischnoneuridae Handlirsch, 1906.

Order Caloneurida Handlirsch, 1906

Family Caloneuridae Handlirsch, 1906

Genus *Eohymen* Martynov, 1937

Eohymen: Martynov, 1937, p. 9.

Type species. *Eohymen maculipennis* Martynov, 1937.

Diagnosis. Wing relatively wide, possibly coriaceous, with deep relief; main veins straight or weakly curved, with dark lines between them, interrupted at boundaries of cells and forming longitudinal impressions close to wing apex. Secondary "costal" vein almost reaching wing middle, ending blindly near anterior wing margin. SC ending near wing apex. RS four-branched. M clearly concave, with narrow short fork. CuA and CuP widely spaced, clearly concave, simple; CuA moderately close to M_5 , with short oblique branch diverging towards it. Postcubital area wide: CuP at level of RS base running almost along middle of wing width. 1A simple; 2A with three terminal branches and many weak, not always regular, oblique S-shaped posterior branches; both anal stems shifting from convex to concave distal to basal quarter of wing. 3A absent or very short. Crossveins simple or Y-shaped, forming network in "precostal" space and, in places, postanal space and forming zigzagging intercalary veins in interrational and intercubital areas.

Species composition. Type species from the Urzhumian Stage of Kargala.

Comparison. The wing venation makes the genus in question very close to *Caloneura* Brongniart, 1885, from which it differs in the presence of the "costal" and intercalary veins, long subcosta, wide postcubital area (in *Caloneura*, the "costal" and intercalary veins are absent, and the postcubital area is narrow). The long "costal" vein distinguishes *Eohymen* from all other Caloneuridae, among which a considerably shorter "C" is only known in *Ligogramma* Béthoux et al., 2004 (Beckemeyer, 2009), *Gigagramma* Béthoux

et al., 2004, and *Paleothygramma acuta* Carpenter, 1943.

Remarks. The genus *Eohymen* was described by Martynov (1937) in the order Palaeodictyoptera (=Dictyoneurida) and transferred by the senior author of this study to Caloneurida (Rasnitsyn et al., 2004). The transfer proposed was not provided with a new reconstruction, giving Béthoux et al. (2004) ground for disagreement. The photograph and reconstruction provided here (Figs. 10a, 10b, 12a) rather convincingly demonstrate the similarity of the venation pattern of *Eohymen* to that of Caloneurida and its difference from that of Dictyoneurida, typically characterized by a distinct division of the media into a convex anterior branch and a concave posterior branch. In the case in question, even if M_5 is taken for MP, the anterior branch of the media is concave and the posterior branch is convex.

Genus *Isadistica* Rasnitsyn et Aristov, gen. nov.

Etymology. From the Isady locality. Gender feminine.

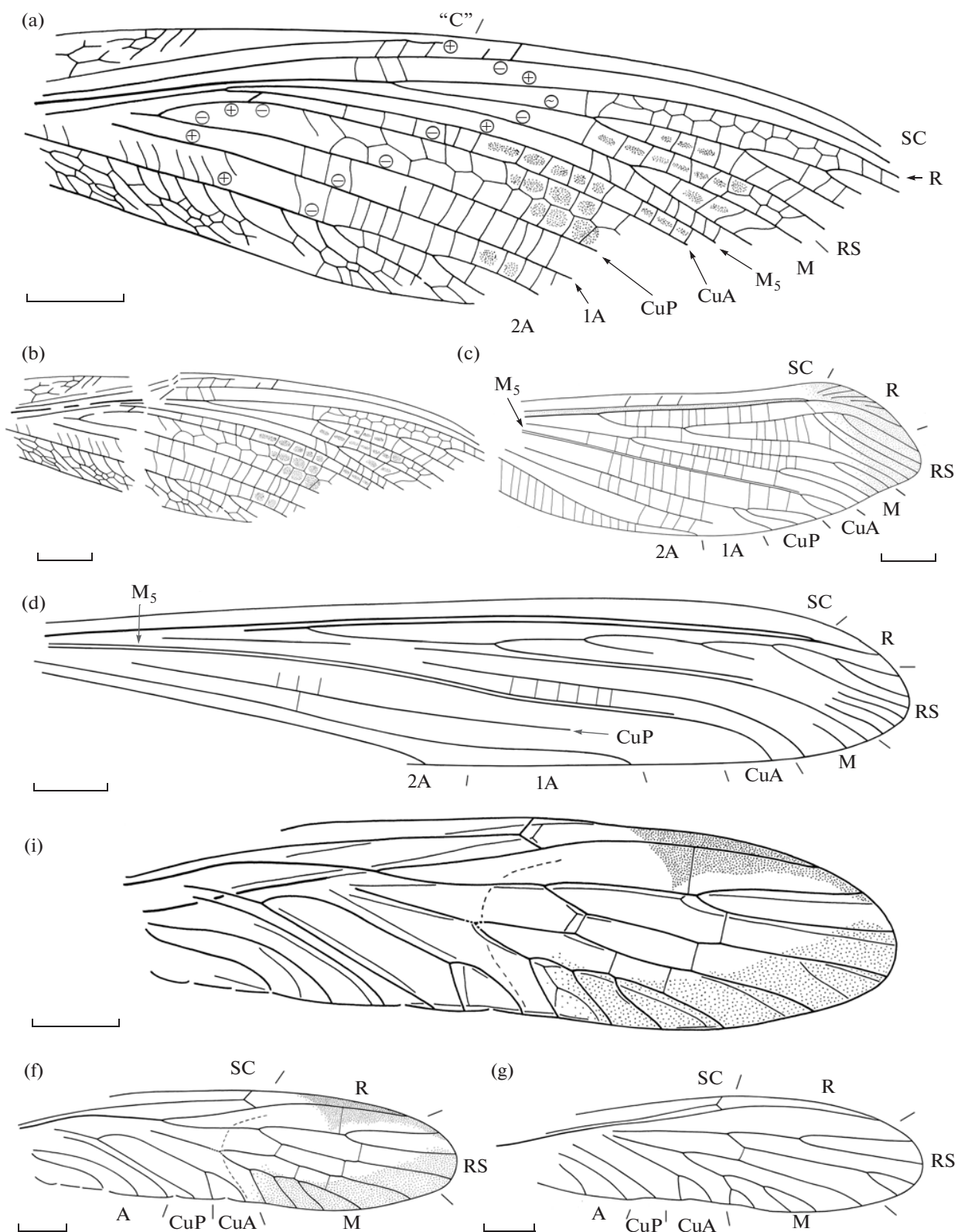
Type species. *I. issada* sp. nov.

Diagnosis. Wing moderately narrow or narrow, with fine veins, mostly straight or weakly curved (more strongly curved near wing apex), branching mainly near wing apex. Anterior wing margin straight, sometimes convex near apex. Costal space and, especially, subcostal space very narrow; costal space dilated distally. SC joining R near wing apex, with short, slightly oblique anterior branches; R distal to apex of SC with closely set oblique branches forming functional pterostigma (known in type species). RS deviating near basal one-third of wing, pectinate, five-branched (in type species); its four apical branches short. M four-branched or three- to four-branched, with proximal bifurcation somewhat distal to base of RS and short apical forks. Convex M_5 and concave CuA set very closely and looking like one vein, convex anteriorly and concave posteriorly, as in hindwings of some Holometabola (*Sialis* Latr., *Corydalus* Latr., *Altajopanorpa* O. Mart., *Permomeropse* Till., and others), with short weak bifurcation near apex. CuP with short weak bifurcations near apex. Two preserved anal veins simple, weakly curved or straight, very long (2A reaching, sometimes far, beyond middle of wing length). Crossveins simple, straight, more or less regular.

Species composition. Two new species described below.

Comparison. The new genus is sharply distinguished from all Caloneuridae by the SC joining R, the very basal position of the bifurcation of M, and M_5 and concave CuA set very closely (turned into one complex vein).

Remarks. Due to the weak morphological differences between the forewing and hindwing in Caloneurida, available material does not allow determining



whether the wings in question are forewings or hindwings. For the same reason, it seems unlikely that the fossils described below represent different wing pairs of the same species, in spite of their comparable size.

Isadistica issada Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. From the village of Isady.

H o l o t y p e. PIN, no. 3840/1701, part and counterpart of incomplete forewing (without base); Isady locality, Vologda Region; Severodvinian Stage.

D e s c r i p t i o n (Figs. 10c, 12b). The wing is approximately 3.5 times as long as wide; its anterior margin is concave near the apex; the apex is somewhat pointed; the posterior margin is weakly convex. The costal space distal to the apex of SC is clearly dilated, darkened, and crossed with closely set oblique veins. The first bifurcation of RS is at the level of the apex of 2A; the others are shifted to the level of the apex of SC and further. The bifurcation of M is closer to the base of RS than to the first bifurcation of RS; the terminal bifurcations are short, especially in the distal branch. CuA is straight, with a very short terminal fork; CuP is weakly curved, with three short terminal branches. 1A is weakly curved; 2A is somewhat more strongly curved; both are simple. The subcostal space, pterostigma area, and wing apex are darkened.

M e a s u r e m e n t s, mm. Length of preserved fragment, 7.4; width, 2.4; estimated forewing length, 8–9.

M a t e r i a l. Holotype.

Isadistica longa Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. Feminine gender form of the Latin *longus* (long).

H o l o t y p e. PIN, no. 3840/684, part and counterpart of slightly distorted wing; Isady locality, Vologda Region; Severodvinian Stage.

D e s c r i p t i o n (Figs. 10d, 12c). The wing is 6.5 times as long as wide, parallel-sided, with almost straight anterior and posterior margins and narrowly rounded, almost symmetrical apex. The costal space proximal to the apex of SC is clearly dilated; here it could have been occupied by densely set not preserved branches of SC, forming the functional pterostigma. The five bifurcations of RS are distributed almost evenly; the first of them is somewhat distal to the middle of the wing; the fifth is distal to the apex of SC. M branches somewhat distal to the base of RS and probably has four ends, but the order of their diversion is unclear. CuA is almost straight almost to the apex;

its apical bifurcation is absent or has not been preserved; CuP, 1A, and 2A are also almost straight, simple (the apex of CuP has not been preserved); 1A is almost parallel to the wing margin distal to the apex of 2A. Coloration is absent (or not preserved).

M e a s u r e m e n t s, mm. Forewing length, 12.5; width, 1.9.

C o m p a r i s o n. The new species differs from the type species in the narrow wing with the nonconcave anterior margin and symmetrical, not pointed apex, the longer SC, the absence of distinct pterostigma, and in the evenly set bifurcations of RS.

M a t e r i a l. Holotype.

Order Hypoperlida Martynov, 1928

Family Hypoperlidae Martynov, 1928

Genus *Idelopsocus* Zalesky, 1929

Idelopsocus mutovinus Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. From the Mutovino locality.

H o l o t y p e. PIN, no. 3840/1650, part and counterpart of overlapping, slightly distorted forewing and hindwing; Isady locality, Vologda Region; Severodvinian Stage.

D e s c r i p t i o n (Figs. 10e–10g; 12d). The wings are long and narrow; the forewing is four times as long as wide. The anterior margin of the forewing is weakly convex, with a barely visible impression distal to the apex of SC. The fork of SC almost reaches the level of the first fork of RS. The pterostigma is not pronounced. RS deviates at the level of the apex of 1A, has three branches; its forks are long and narrow; the stem of RS_{1+2} is slightly shorter than the subequal stems of RS and RS_1 . M branches somewhat distal to the bifurcation of CuA; its anterior branch is simple, almost straight; its posterior branch forms a comb of four short branches. The fork of CuA is small, its length along the wing margin is considerably smaller than one-third of the wing width in this area. The anal veins are straight almost to the level of the bifurcation of CuA, weakly diverging and, then, smoothly curving posteriad; 2A has a short posterior branch. The preserved crossveins are the following: r-rs (proximal to the bifurcation of RS_{1+2}), r_2 – r_3 , and two of both r-m and m_1 – m_2 . The distal half of the wing is darkened along the margin and has an incomplete darkened transverse stripe distal to the clearly pronounced nodal line; the darkening is especially strong in the pterostigma area. The hindwing is probably not darkened, similar in venation to the forewing, but, in addition to the usual differences of hindwings from forew-

Fig. 10. Members of Caloneurida and Hypoperlida: (a, b) *Eohymen maculipennis* Martynov, 1937, holotype PIN, no. 100/2, forewing; Kargala locality, Orenburg Region; Urzhumian Stage: (a) reconstruction, (b) preserved venation; (c) *Isadistica issada* sp. nov., holotype PIN, no. 3840/1701, forewing; Isady locality, Vologda Region; Severodvinian Stage; (d) *I. longa* sp. nov., holotype PIN, no. 3840/684, forewing; Isady locality, Vologda Region; Severodvinian Stage; (e–g) *Idelopsocus mutovinus* sp. nov., holotype PIN, no. 3840/1650, Isady locality, Vologda Region; Severodvinian Stage: (e) overlapping fore- and hindwings; (f) forewing; (g) hindwing. Scale bars: (a, b) 5 and (c–g) 1 mm.

ings (narrow preradial space, more proximally deviating RS), has M_2 dichotomizing instead of pectinate.

Measurements, mm. Forewing length, 8.5; width, 2.3.

Comparison. The new species is clearly distinguished from all congeners by the multibranch posterior branch of M (four branches instead of two), the small fork of CuA , and narrow and long wing.

Remarks. The multibranch posterior branch of M is unusual not only to the genus *Idelopsocus*, but also largely to the whole family Hypoperlidae (sensu Shcherbakov, 1995). However, the venation of hypoperlids is subject to aberrant variation (Shcherbakov, 1995); therefore, it seems untimely to erect a special genus for the new species, until the stability of this character is confirmed by further findings.

Family Ischnoneuridae Handlirsch, 1906

Ischnoneuridae: Handlirsch, 1906a, p. 134.

Adiphebiidae: Handlirsch, 1906b, p. 712 (syn. nov.).

Anthracoptilidae: Handlirsch, 1922, p. 98 (syn. nov.).

Permarrhaphidae: Martynov, 1931, p. 190 (syn. nov.).

Strephocladidae: Martynov, 1938a, p. 100.

Strephoneuridae: Martynov, 1940, p. 14.

Generic composition. *Ischnoneura* Brongniart, 1893, *Anthracoptilus* Laméere, 1917, *Mesoptilus* Laméere, 1919, *Pseudooedischia* Handlirsch, 1919 from the Upper Carboniferous of France; *Adiphebia* Scudder, 1885 from the Upper Carboniferous of the United States; *Strephocladus* Scudder, 1885 from the Upper Carboniferous of Germany; *Carrizocladus* Rasnitsyn in Rasnitsyn et al., 2004 from the Permian–Carboniferous boundary beds of the United States; *Spargoptilon* Kukalová, 1965 from the Lower Permian of the Czech Republic; *Homocladus* Carpenter, 1966 and *Paraccladus* Carpenter, 1966 from the Lower Permian of the United States; *Mycteroptila* Rasnitsyn, 1977, *Rhinomaloptila* Rasnitsyn, 1977 from the Lower Permian of the Russia; *Graticladus* Novokshonov et Aristov, 2004, *Permarrhaphus* Martynov, 1931, and *Strephoneura* Martynov, 1940 from the Middle Permian of Russia; *Strephoptilus* Rasnitsyn et Aristov, gen. nov. from the Upper Permian of European Russia; *Jarmilacladus* Rasnitsyn et Aristov, 2004 from the Middle Permian of Russia and Upper Permian of Australia.

Remarks. The genus *Ischnoneura* Brongniart, 1893 (Fig. 11a) is included in this family and, thus, Anthracoptilidae is synonymized under Ischnoneuridae based on the following combination of characters of this genus, which make it similar to anthracop-

tilids and distinguish it from Cnemidolestidae (order Eoblattida), to which *Ischnoneura* was previously considered to be close (Béthoux, 2005):

— R has a posterior branch in the fore- and hindwings, which is uncharacteristic of cnemidolestids, but typical, e.g., of such anthracoptiline as *Strephoneura* Martynov, 1940.

—The distal portion of the anterior margin is identical in the fore- and hindwings, which is uncharacteristic of cnemidolestids, but typical of those anthracoptilids in which hindwings are sufficiently well known (*Strephoneura*).

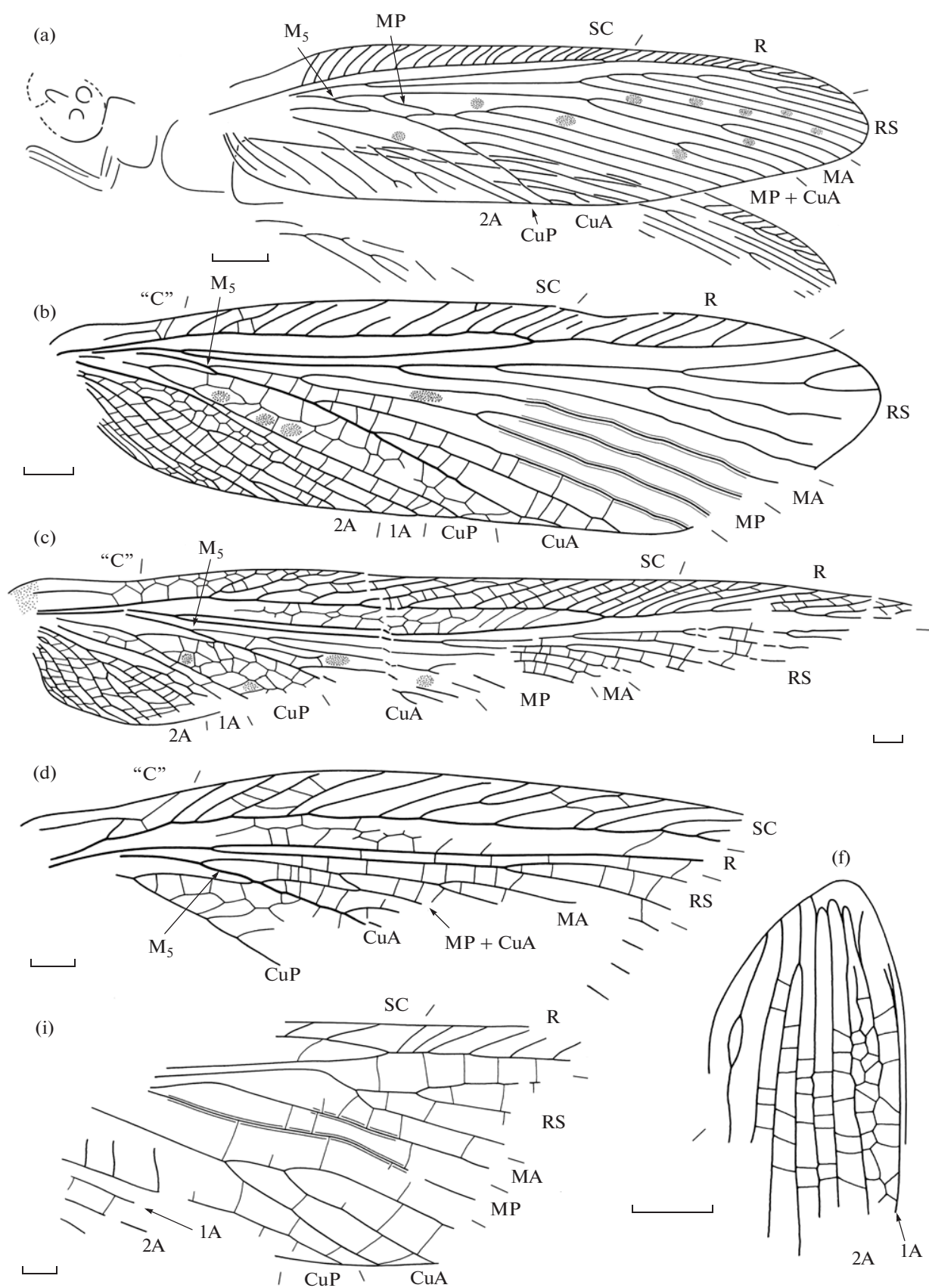
—The anterior branch of CuA is not bent far anteriorly, so that the anterior margin of the cubital system is not S-shaped, as is characteristic of cnemidolestids.

—The forelegs are absolutely not enlarged, in contrast to the huge raptorial forelegs of cnemidolestids (see Béthoux and Nel, 2005). In anthracoptilids, the forelegs are invariably rather small (somewhat shorter or longer than the midlegs, but invariably much smaller than hindlegs). They are sometimes interpreted as raptorial (in *Mesoptilus* Laméere, 1917; Béthoux and Wieland, 2009), but in most cases (in *Anthracoptilus* Laméere, 1917, *Mycteroptila* Rasnitsyn, 1977, and *Rhinomaloptila* Rasnitsyn, 1977), they are typical clinging legs.

Ischnoneura is considered to be close to cnemidolestids based on the MP joining CuA , but, in cnemidolestids, this fusion looks different: they have a free MP always weak, often with sharp bends at points where crossveins join it, and, if it is not lost among crossveins, joining CuA rather distally (never proximal to the first bifurcation). In *Ischnoneura*, as in *Strephoptilus* gen. nov., MP joins the first branch of CuA . *Ischnoneura* is considered to be close to the former Anthracoptilidae, rather than Tococladidae, in spite of the simple weakly inclined branches of SC , which are characteristic of the latter family, because of the similarity of this genus to *Strephoneura* and *Strephoptilus* (see above) and because of the absence of an unusual shape of RS characteristic of *Tococladus* Carpenter, 1976 and *Opisthocladus* Carpenter, 1976 (see below). These characters actually cast doubt on the distinctions between these families, but until more detailed information on Tococladidae and, especially, on the genus *Opisthocladus* is available, it seems premature to synonymize these families.

Otherwise, the diagnosis and size of the family are understood here mostly in the same way as in our previous study (Rasnitsyn and Aristov, 2004), with the fol-

Fig. 11. Members of Hypoperlida: (a) *Ischnoneura oustaleti* (Brongniart, 1885), holotype Muséum national d'histoire naturelle, DHT-R51077, habitus; Commeny locality, France; Stephanian Stage of the Upper Carboniferous (orig. drawing from photograph in Brongniart, 1885, tabl. XXI, fig. 4); (b–d) *Strephoptilus* gen. nov., Isady locality, Vologda Region; Severodvinskian Stage: (b) *S. borealis* sp. nov., holotype PIN, no. 3840/1651, forewing; (c, d) *S. longus* sp. nov.: (c) holotype PIN, no. 3840/1652, forewing; (d) specimen PIN, no. 3840/1654, forewing; (e) *?Jarmilacladus patiens* sp. nov., holotype PIN, no. 3286/134, clavus; Chepanikha locality, Udmurtia; Urzhumian Stage; (f) *Opisthocladus kargalensis* sp. nov., holotype PIN, no. 199/374, forewing; Kargala locality, Orenburg Region; Urzhumian Stage. Scale bars: (a) 5 and (b–f) 1 mm.



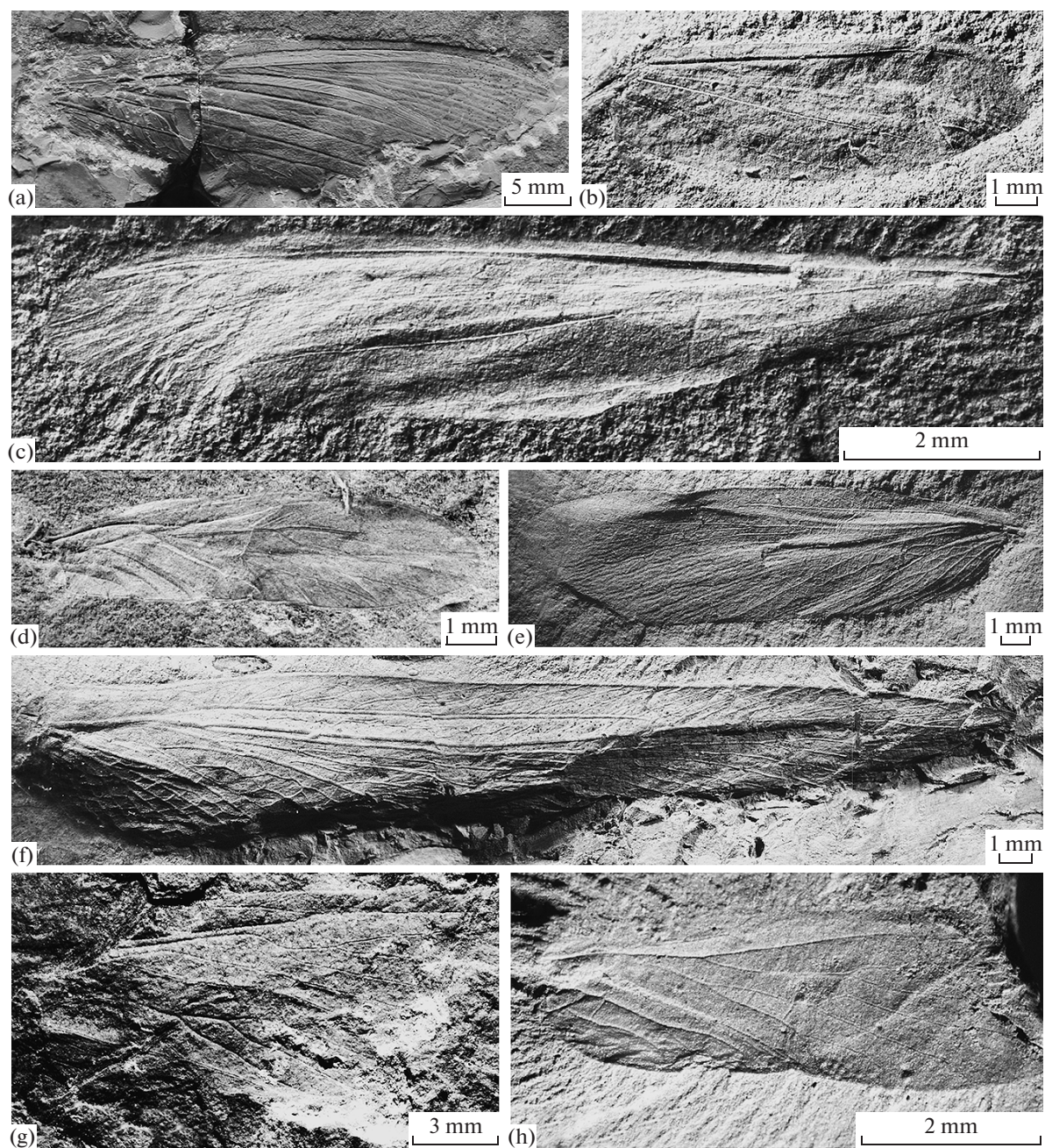


Fig. 12. Members of Caloneurida, Hypoperlida, and Palaeomanteida: (a) *Eohymen maculipennis* Martynov, 1937, holotype PIN, no. 100/2, forewing; Kargala locality, Orenburg Region; Urzhumian Stage; (b) *Isadistica issada* sp. nov., holotype PIN, no. 3840/1701, forewing; Isady locality, Vologda Region; Severodvinian Stage; (c) *I. longa* sp. nov., holotype PIN, no. 3840/684, forewing; Isady locality, Vologda Region; Severodvinian Stage; (d) *Idelopsocus mutovinus*, sp. nov., holotype PIN, no. 3840/1650, overlapping fore- and hindwing; Isady locality, Vologda Region; Severodvinian Stage; (e) *Strephoptilus borealis* sp. nov., holotype PIN, no. 3840/1651, forewing; Isady locality, Vologda Region; Severodvinian Stage; (f) *S. longus* sp. nov., holotype PIN, no. 3840/1652, forewing; Isady locality, Vologda Region; Severodvinian Stage; (g) *Opisthocladus kargalensis* sp. nov., holotype PIN, no. 199/374, forewing; Kargala locality, Orenburg Region; Urzhumian Stage; (h) *?Miomatoneurella rossoshana* sp. nov., holotype PIN, no. 3286/119, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

lowing modifications. The genus *Opisthocladus* is returned from Anthracoptilidae to the family Tococladidae, since its anterior branches of SC are simple and

short, except for the most basal one, and RS is similar in extraordinary shape to *Tococladus* (see below). In addition to the new genus *Strephoptilus*, along with

Pseudooedischia, *Carrizocladus*, and *Graticladus*, which were omitted by or not yet known to the authors at the time of that publication, and to *Homocladus*, which was erroneously synonymized in that publication (see below), the genus *Adiphlebia* Scudder, 1885 from the Upper Carboniferous Mazon Creek locality, United States, is also included in Ischnoneuridae. The redescription of the type species (Béthoux, 2009; Kukalová and Beutel, 2012) and our data show its wing venation as characteristic of Ischnoneuridae. Kukalová and Beutel (2012) transferred *Adiphlebia* to Strephocladidae (and by inference to Ischnoneuridae) which we agree completely with.

The proposal to exclude the genus *Mesoptilus* Laméere, 1919 from Hypoperlida based on the argument that “*Mes. dolloi* and its Palaeozoic relatives can be considered as stem-Mantodea on the basis of two forewing character states: anterior branch of M fused with RP for a long distance (completely fused in crown-Mantodea; as opposed to M and RP distinct); and CuA₂ anteriorly pectinate (as opposed to posteriorly pectinate, or no consistent branching pattern)” (Béthoux and Wieland, 2009: p. 104–105), also cannot be accepted. First, this hypothesis discards abundant evidence of the affinity of Manteida to Blattida and, in particular, to certain advanced groups of Mesozoic Blattida (Vršanský, 2002; Grimaldi and Engel, 2005; Kukalová and Beutel, 2012). Second, it contradicts the rather obvious relationships of ischnoneurids with other Hypoperlidae and, through them, on the one hand, with booklice and homopterans and, on the other hand, with paleodictyopteroids (see Rasnitsyn, 1980; Rasnitsyn and Quicke, 2002). Third, ischnoneurids include forms (e.g., *Strephoneura* Martynov, 1940 and *Mycteroptila armipotens* Novokshonov, 1998) with the typical rooflike position of wings at rest (see Rasnitsyn, 1980, text-fig. 24; Rasnitsyn and Quicke, 2002, text-figs. 131, 132), which is impossible for Gryllones. And, finally, this hypothesis does not propose transitional forms between Paleozoic ischnoneurids and Mantodea, which have not been recorded from deposits earlier than the terminal Jurassic, in contrast to the traditional hypothesis, according to which transitional forms between Blattida and Mantodea are quite obvious (Vršanský, 2002; Grimaldi and Engel, 2005).

Genus *Strephoptilus* Rasnitsyn et Aristov, gen. nov.

Etymology. From the Greek *strepho* (turn, twist) and *ptilon* (feather, wing). Gender masculine.

Type species. *S. borealis* sp. nov.

Diagnosis. SC joining R; branches of SC rather short, relatively weakly inclined, more or less regularly positioned. RS deviating at level of, or proximal to, M₅. RS and MA not anastomosing. R without separate posterior branch near apex. Intercubital space with two or three rows of irregular cells. 1A simple; 2A pectinate or irregularly branching. Pronounced intercalary veins absent.

Comparison. The new genus differs from the majority of genera in the relatively short and less inclined, more regular branches of SC; it is similar in this respect to *Ischnoneura* Brongniart, 1893 and *Graticladus* Aristov et Novokshonov, 2004, providing, along with them the transition to the family Tococladidae (and, thus, strengthening the doubts about their status as a separate family). Additionally, it is similar to *Ischnoneura* and *Graticladus* in the very proximally deviating RS and the absent of an anastomosis of RS and MA; it is also similar to *Ischnoneura* in the tendency (realized in interspecific variation) to form an anastomosis between MP and the anterior branch of CuA and in the coloration pattern in the form of rather infrequent small rounded dark spots. In contrast to *Ischnoneura*, R lacks a distinct posterior branch near the apex. In contrast to *Graticladus*, 1A is simple, and 2A is not so broadly and regularly pectinate. In contrast to *Jarmilacladus*, SC is fused into R.

Species composition. Two new species described below.

Strephoptilus borealis Rasnitsyn et Aristov, sp. nov.

Etymology. From the Latin *borealis* (northern).

Holotype. PIN, no. 3840/1651; part and counterpart of complete, somewhat distorted forewing; Isady locality, Vologda Region; Severodvinskian Stage.

Description (Figs. 11b, 12e). Moderately large forewing with oblique, not long, mostly simple anterior branches of SC. SC is fused into R at about 0.6 of the wing length. RS is not entirely regularly pectinate from the middle of the wing and has six ends. M branches not far behind M₅; MA is simple; MP is free, with a bifurcation. CuA is pectinate anteriorly, three-branched. CuP is simple, straight. The anterior margin of the clavus is weakly convex; 2A is four-branched; the other five or six anal veins are simple, weakly S-shaped. M and, partially, RS and CuA in the distal portion of the wing are bordered by fine grooves on both sides. The crossveins are not quite regular; in the subcostal, intercubital, and anterior interanal spaces, they form three rows of cells. The rather small oval dark spots are distinct: one in the intermedial space and three in the intercubital space.

Measurements, mm. Forewing length, 17; width, 4.7.

Remarks. Judging from the size, two other distorted forewing fragments probably also belong to this species. One (specimen PIN, no. 3840/1653) is larger than the holotype (estimated wing length 22–23 mm) and lacks preserved coloration. The second (specimen PIN, no. 3840/1656) is incomplete and crumpled, with a greater number of dark spots, possibly represents a separate species, which is not established because of poor preservation.

Material. In addition to the holotype, probably also specimens PIN, nos. 3840/1653 and 1656 from

the same locality, not included in the type series because of their poor preservation.

Strephoptilus longus Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. From the Latin *longus* (long).

H o l o t y p e. PIN, no. 3840/1652; part and counterpart of forewing without apex and most of posterior margin; Isady locality, Vologda Region; Severodvinian Stage.

D e s c r i p t i o n (Figs. 11c, 11d, 12f). Large forewing with mostly simple anterior branches of SC more inclined and longer than in the type species. SC is fused with R distal to the middle of the wing length. RS is not entirely regularly pectinate and has at least seven ends. The branching pattern of M is possibly similar to that of the type species, except for MP, which is probably fused with the anterior branch of CuA. CuA has at least three free branches. The anterior margin of the clavus is weakly convex; 1A is simple, weakly curved; 2A has five branches; the next five anal veins are simple, weakly S-shaped. Crossveins are not entirely regular; in the basal part of the costal space and in the subcostal space, they form two rows of cells and, in the intercubital space, they form three rows of cells. Rather small oval dark spots are preserved in the mediocubital and intercubital spaces (two such spots in each space).

M e a s u r e m e n t s, mm. Length of incomplete forewing, 31; estimated total length, about 33–35.

C o m p a r i s o n. The new species is distinguished from the type species by the large size, more strongly inclined branches of SC, and the greater number of branches of RS and, possibly, CuA.

R e m a r k s. Judging from the large size, two other fragments possibly also belong to this species: the wing base (specimen PIN, no. 3840/1654) with MP distinctly fused with the anterior branch of CuA (Fig. 11d) and a fragment of the posterior forewing margin (specimen PIN, no. 3840/1655).

M a t e r i a l. In addition to the holotype, specimens PIN, nos. 3840/1654 and 1655 from the same locality, not included in the type series because of their poor preservation.

Genus *Jarmilacladus* Rasnitsyn et Aristov, 2004

?*Jarmilacladus patiens* Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. The Latin *patiens* (patient).

H o l o t y p e. PIN, no. 3286/134; part and counterpart of incomplete forewing clavus; Chepanikha locality, Udmurtia; Urzhumian Stage.

D e s c r i p t i o n (Figs. 11d). Incomplete clavus of a relatively large wing, with nine weakly diverging veins, mostly with independent bases (the sixth and seventh veins with a short common base); 2A is soon lost in the network; behind it, there is a short intercalary vein; otherwise, there are simple crossveins between the longitudinal veins.

M e a s u r e m e n t s, mm. Length of fragment, 4.7; width of clavus near base, 2.5.

C o m p a r i s o n. The new species is distinguished from the type species by the presence of only one short intercalary vein in the clavus and by the smaller size. In the type species *J. variabilis* Rasnitsyn et Aristov, 2004, there are several intercalary veins and the clavus is twice as wide (Rasnitsyn and Aristov, 2004).

R e m a r k s. This fragment is assigned to the family Ischnoneuridae and, provisionally, to the genus *Jarmilacladus* based on considerable similarity in the clavus shape. In other genera of the family in which the clavus is known, it usually has a different structure (with branching and/or variously fused anal veins). A more similar clavus, with more or less parallel, nonbranching or almost nonbranching veins, with intercalary veins or without them, and without a network of cells, is known in *Adiphebia lacoana* Scudder, 1885, *Homocladus grandis* Carpenter, 1966, and *Permarrhaphus venosus* Martynov, 1931, but, in the first two species, the clavus has much more intercalary veins and, in *Permarrhaphus*, the clavus is considerably less polynervous.

In this connection, it should be noted that synonymization of *Homocladus* Carpenter, 1966 under *Spargoptilon* Kukalová, 1965 (Rasnitsyn in Rasnitsyn et al., 2004) was erroneous. In *Spargoptilon*, M_5 is fused into CuA proximal to its division into branches, while, in *Homocladus* (as in *Paracladus* Carpenter, 1966, *Jarmilacladus*, and *Strephoneura*), it is fused into the anterior branch of CuA.

A clavus of a rather similar structure is figured along with the description of *Ideloblatta rossica* M. Zalesky, 1929 (Zalesky, 1929, text-fig. 4), although it lacks intercalary veins and has only simple crossveins. The systematic position of this insect is uncertain and can hardly be clarified without studying the type specimen, but its place in Ischnoneuridae remains possible.

In Blattida and Eoblattida, the clavus looks considerably different: it is more lanceolate, with more strongly curved veins (especially 1A) and often more strongly tending to branch.

M a t e r i a l. Holotype.

Family Tococladidae Carpenter, 1966

The separate status of this family requires confirmation (see above). The family is considered to comprise two genera, *Tococladus* Carpenter, 1966 and *Opisthocladus* Carpenter, 1976 from the Permian deposits of Europe and North America.

Genus *Opisthocladus* Carpenter, 1976

Opisthocladus kargalensis Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. From the Kargala locality.

Holotype. PIN, no. 199/374; counter impression of forewing without base and apex; dumps of Kargala Copper Mines, Sakmarskii District, Orenburg Region; Amanak Formation, Middle Permian.

Description (Figs. 11f, 12g). The costal space includes medially simple oblique branches of SC and R, forming a dense pattern just distal to the apex of SC. The subcostal space includes at least one (distal) crossvein. RS approaches R, almost touching it over most of the preserved fragment, bends posteriad ("deviates from R") proximal to the apex of SC, and has two posterior branches near the base (the base of the first branch is proximal to the apex of SC). M has a bifurcation markedly basal to the base of RS; other bifurcations in the preserved part of the wing are absent; both main branches within a short segment (MA) or almost the whole of visible length (MP) run along the bottom of a longitudinal impression bordered by fine lines. CuA is strongly convex, with a long straight stem and posterior comb of three closely set branches; both bifurcations of CuA are between the bifurcation of M and the base of RS. CuP is almost straight, simple, closely approaching the level of the base of RS. The anal veins are straight, at least three in number, probably independently reaching the posterior wing margin. The crossveins are simple, straight, less often, oblique.

Measurements, mm. Length of fragment, about 13; estimated wing length, at least 20; wing width, 6.

Comparison. The new species differs from other species known from Leonardian deposits of Kansas, United States, in the RS basally set very closely to R, the proximal branching of RS and M, closely positioned anterior branches of R immediately distal to the apex of SC, and in the larger size; it also differs from *O. arcuatus* Carpenter, 1976 in the presence of crossveins in the subcostal space, at least three-branched RS, and the longer CuP. Additionally, it differs from *O. strictus* Carpenter, 1976 in the three-branched CuA with a long straight stem. In the American species, RS branches distal to the apex of SC; M branches approximately at the same level as CuA, and the wing is 13–15 mm long. In *O. arcuatus*, the subcostal space lacks crossveins; RS has two branches; and CuP terminates far from reaching the level of the apex of SC. In *O. strictus*, CuA is four-branched, with a short stem. In both American species, RS diverges immediately from R and does not approach it basally (Carpenter, 1976).

Remarks. RS approaching basally R is characteristic of species of *Tococladus*; however, the posteriorly pectinate CuA confirms that the new species belongs to *Opisthocladus*.

Material. Holotype.

Order Palaeomanteida Handlirsch, 1906

Remarks. Following the description of new members of the order Miomoptera (=Palaeo-

manteida), the system of this order at the level of families, especially the limits of the family Permosialidae and a number of other groups became strongly blurred (cf. Rasnitsyn, 1980; Storozhenko and Novokshonov, 1999; Rasnitsyn and Quicke, 2002; Novokshonov and Zhuzhgova, 2004; Rasnitsyn et al., 2004). The only reliable fact is the separate status of the family Permembidae, recently transferred to this order from Grylloblattida (Aristov and Rasnitsyn, 2008). The traditional miomopterans, for which rather many family names have been proposed (Palaeomanteidae Handlirsch, 1906, Delopteridae Sellards, 1909, Epimastacidae Martynov, 1928, Permosialidae Martynov, 1928, Palaeomantiscidae Rasnitsyn, 1977, Permonkidae Rasnitsyn, 1977, Tologopteridae Storozhenko, 1992, and Perloblattidae Storozhenko, 1992) have a standard venation in forewings, which provide the bulk of fossil specimens of this order. Distinctive features of the body of some taxa (such as the three-segmented tarsi in *Permosialis* Martynov, 1928 and five-segmented tarsi in *Palaeomantina* Rasnitsyn, 1977; the strong saltatorial legs of *Sellardsiopsis* G. Zalesky, 1939, the type genus of the family Palaeomantiscidae; the flat position of wings at rest and extraordinary hindwing venation in *Permonka* Riek, 1973), were they better studied, could well provide the foundation for constructing a more differentiated system of the order. However, at the current level of knowledge, the system of the order should be constructed based on the characters found in the most representative material, i.e., the forewing. Among the forewing characters, probably only the mutual positions of the stems of M and CuA at the base of the wing, along with the simple CuA, which characterizes Permembidae, are promising for dividing the diversity of miomopterans into groups of comparable size. In *Epimastax* Martynov, 1928, *Permosialis* Martynov, 1928, and *Permonka* Riek, 1973, these stems are either free (connected by a short M_3) or fused for a short distance at the wing base, while in numerous genera of Palaeomanteidae (including Delopteridae) and, in *Sellardsiopsis* and *Palaeomantina*, M and CuA are fused for a longer distance and diverge farther from the wing base. Based on this character, we provisionally divide the order into three families: Palaeomanteidae Handlirsch, 1906, Permosialidae Martynov, 1928, and Permembidae Tillyard, 1937. The composition of Permosialidae accepted here was principally proposed by Storozhenko and Novokshonov (1999), but, unlike these authors, we assign *Permonia* Kukalová, 1963, which has a long M + CuA, to Palaeomanteidae.

Family Palaeomanteidae Handlirsch, 1906

Palaeomanteidae: Handlirsch, 1906, p. 348.

Delopteridae: Sellards, 1909, p. 168.

Palaeomantiscidae: Rasnitsyn, 1977, p. 75.

Diagnosis. Forewing with M and CuA fused for long distance and diverging far from wing base (nor-

mally, distal to middle of anal space); CuA with bifurcation.

Generic composition. *Palaeomantis* Handlirsch, 1906, *Delopterus* Sellards, 1909, *Miomatoneura* Martynov, 1927, *Delopsocus* Tillyard, 1928, *Sellardsiopsis* G. Zalessky, 1939, *Miomatoneurella* O. Martynova, 1958, *Permonia* Kukalová, 1963, *Perunopterus* Kukalová, 1963, *Permodelopterus* Kukalová, 1963, *Saariomoptera* Guthörl, 1963, *Palaeomantina* Rasnitsyn, 1977, *Delopterinus* Rasnitsyn in Rasnitsyn et al., 2004, *Neodelopterus* Rasnitsyn in Rasnitsyn et al., 2004, *Stigmodelopterus* Rasnitsyn in Rasnitsyn et al., 2004, and *Tridelopterus* Rasnitsyn in Rasnitsyn et al., 2004 from the Upper Carboniferous and Permian of Eurasia and North America.

Comparison. The family is distinguished from Permosialidae by the long anastomosis of M + CuA and from Permembidae by the bifurcation of CuA.

Genus ?*Miomatoneurella* O. Martynova, 1958

?*Miomatoneurella rossoshana* Rasnitsyn et Aristov, sp. nov.

Etymology. From the Rossokha River (stem: rossosh).

Holotype. PIN, no. 3286/119, part and counterpart of incomplete forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 12h, 13a). The forewing has a rounded dark spot in the interrarial and radio-medial spaces proximal to the bifurcations of RS and M, ruptured along the stem of RS, and an anal space broadly (almost to the anal bifurcations) darkened along the posterior margin. SC lacks anterior branches, terminates in a fork near the basal one-third of the wing length, approximately at the level of the apex of 1A; distal to it, R has an oblique anterior vein at the level of the bifurcation of M. The bifurcation of RS is somewhat distal to the bifurcation of M; the number of branches of RS (two or more) is unknown. The crossvein r-rs is located immediately distal to the bifurcation of RS; rs-m (the false base of MA at RS) is positioned proximal to this bifurcation; both crossveins are weakly oblique; MA is angularly curved at rs-m. The bifurcation of M + CuA is positioned slightly distal to the base of RS; the fork of CuA is short and broad; CuA₁ is angulate near the crossvein mp-cua1. Both 1A and 2A have a bifurcation. Additional simple crossveins are discernible between M, CuA, CuP, 1A, and 2A.

Measurements, mm. Length of impression, 6; estimated wing length, about 7; width, 2.2.

Comparison. The new species differs from congeners and most or even all other Palaeomanteidae in the broad angular bifurcation of CuA, which is more characteristic of Hypoperlida and early Psocida.

Remarks. The only known impression is incompletely preserved, so that it is possible that RS had a third branch, which is characteristic of the closely related genus *Miomatoneura* Martynov, 1927. However, the short SC suggests that it is less probable the new species belongs to this genus.

Material. Holotype.

Genus ?*Tridelopterus* Rasnitsyn in Rasnitsyn et al., 2004

?*Tridelopterus indebitum* Rasnitsyn et Aristov, sp. nov.

Etymology. The Latin *indebitum* (improper, undue).

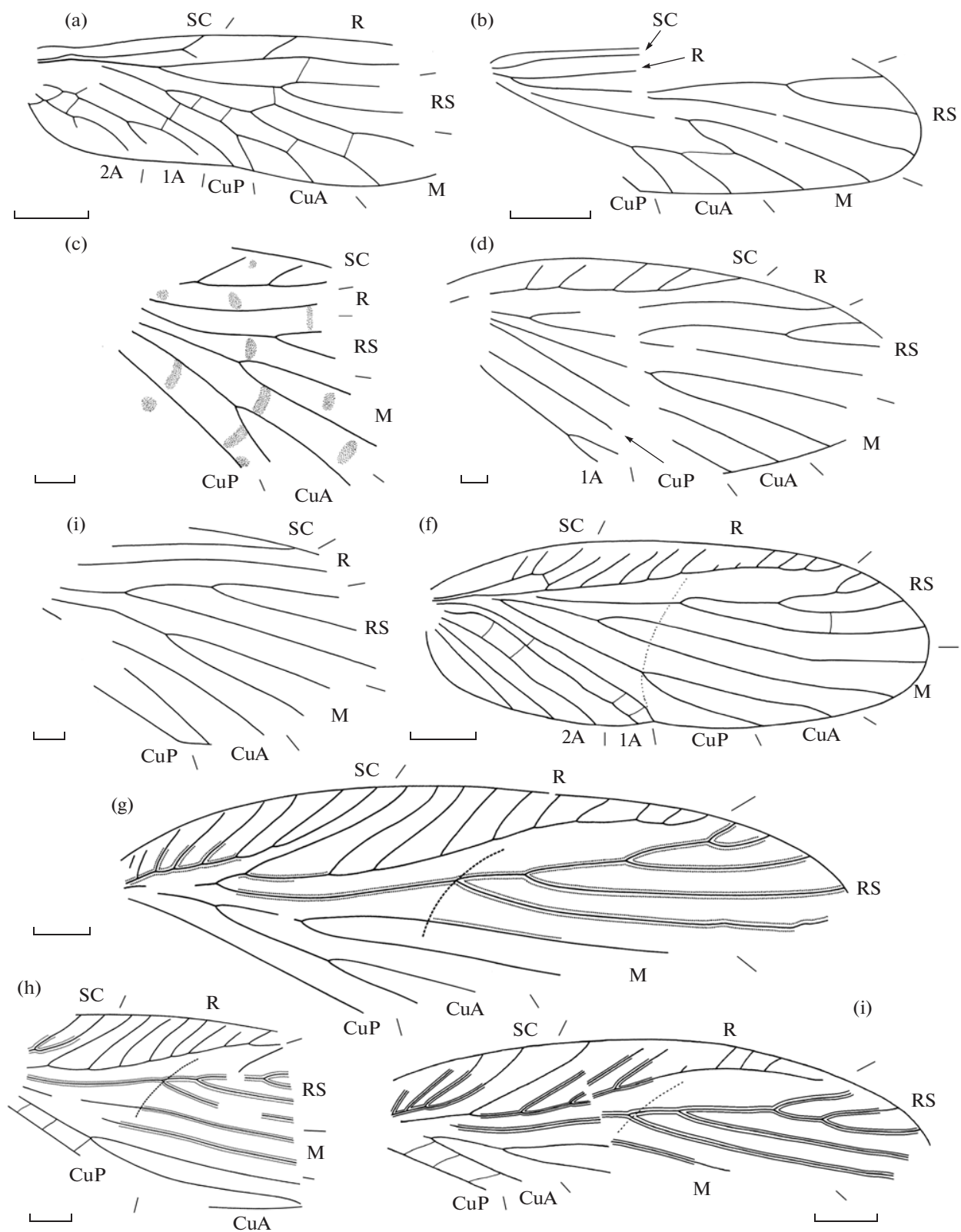
Holotype. PIN, no. 3840/1029, part and counterpart of incomplete hindwing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 13b, 15a). The hindwing lacks a coloration pattern. SC lacks anterior branches in the basal part of the wing. RS deviates at the level of the basal bend of SC and has three branches; the first branch diverges proximal to the middle of the wing; the second bifurcation is in the distal quarter of the wing. M is free at the level of the base of RS; its bifurcation is near the middle of the wing length. The stem of CuA is almost straight; its bifurcation is somewhat proximal to the bifurcation of RS, with two free branches and apex fused with MP; the distances between the apices of M and CuA at the wing margin are almost equal. The anal veins and most of CuP are not preserved.

Measurements, mm. Hindwing length, 6.0.

Comparison. The new species is similar to the type species *T. variegatum* Rasnitsyn, 2004 (in Rasnitsyn et al., 2004) in the combination of the three-branched RS and three-branched CuA in the hindwing and is clearly distinguished by the fusion of the distal branch of CuA with MP, while, in the type species, this branch is free. Additionally, it is distinguished by the absence of the variegated coloration pattern characteristic of the type species and by the much more distal position of the bifurcation of M (in *T. variegatum*, it is positioned proximal to the bifurcation of CuA).

Fig. 13. Members of the families Palaeomanteidae and Permosialidae (Palaeomanteida): (a) ?*Miomatoneurella rossoshana* sp. nov., holotype PIN, no. 3286/119, forewing; Udmurtia, Chepanikha locality, Urzhumian Stage; (b) ?*Tridelopterus indebitum* sp. nov., holotype PIN, no. 3840/1029, hindwing; Isady locality, Vologda Region; Severodvinian Stage; (c) *Permosialis zavialovensis* sp. nov., holotype PIN, no. 3286/124, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (d) *P. udmurtensis* sp. nov., holotype PIN, no. 3286/123, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (e) *Permosialis* sp., specimen PIN, no. 3695/5, hindwing; Kostovaty locality, Udmurtia; Urzhumian Stage; (f) *Epimastax tshepanikha* sp. nov., holotype PIN, no. 3286/125, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (g–i) *E. mutovinensis* sp. nov., Isady locality, Vologda Region; Severodvinian Stage; (g) holotype PIN, no. 3840/1660, forewing; (h) specimen PIN, no. 3840/2078, forewing; (i) specimen PIN, no. 3840/559, forewing. Scale bars in Figs. 13, 14, 16–18, 1 mm.



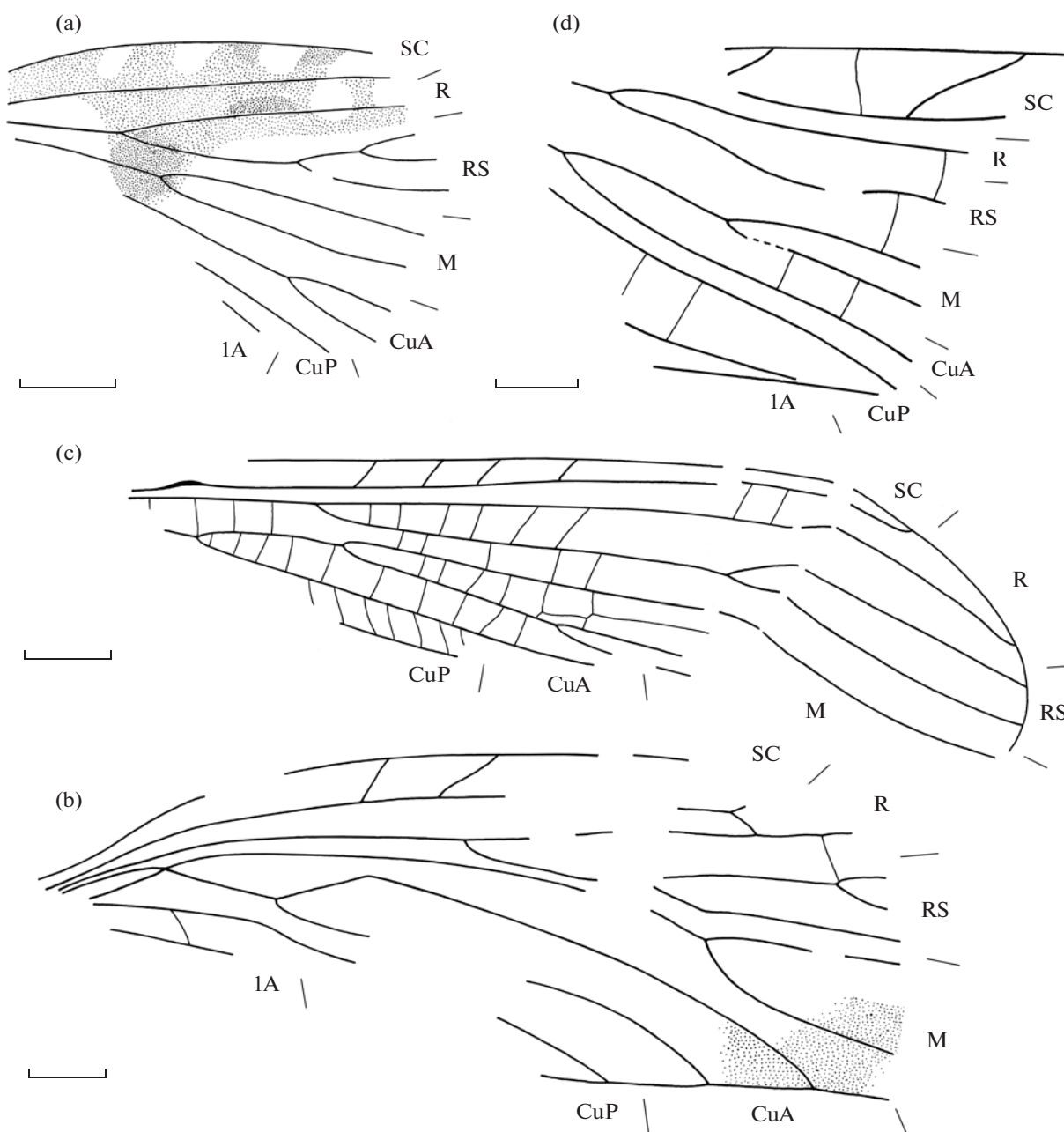


Fig. 14. Members of the families Permosialidae and Permembaliidae (Palaeomanteida), forewings: (a) *Balymotikha deterior* sp. nov., holotype PIN, no. 5103/20, Vyazniki locality, Vladimir Region; Vyatkian Stage; (b) *Onthomastax coprinus* sp. nov., holotype PIN, no. 3286/146, Chepanikha locality, Udmurtia; Urzhumian Stage; (c) *Issadembia infracta* sp. nov., holotype PIN, no. 3840/1667, Isady locality, Vologda Region; Severodvinian Stage; (d) *Neembia ampla* sp. nov., holotype PIN, no. 3840/1670, Isady locality, Vologda Region; Severodvinian Stage.

Remarks. The differences between the new and type species are rather of generic level; however, the establishment of a new genus is premature because of the incompletely preserved specimen and lack of information on the morphology of hindwings (most of the Palaeomanteida are described from forewings).

Material. Holotype.

Family Permosialidae Martynov, 1928

Permosialidae: Martynov, 1928, p. 93.

Epimastacidae: Martynov, 1928, p. 62.

Permonkidae: Rasnitsyn, 1977, p. 72.

Perloblattidae: Storozhenko, 1992a, p. 75.

Tologopteridae: Storozhenko, 1992b, p. 126.

Diagnosis. Forewing with M and CuA free at base (connected by short M_5) or fused over short seg-

ment and diverging before middle of anal space. CuA two-branched.

Generic composition. *Permosialis* Martynov, 1928 (= *Sarbalopterodes* Storozhenko, 1991 = *Tologoptera* Storozhenko, 1992), *Epimastax* Martynov, 1928, *Permonikia* Kukalová, 1963, *Permonka* Riek, 1973 (= *Perloblatta* Storozhenko, 1992), and *Onthomastax* gen. nov. from the Permian, Triassic, and Jurassic of Eurasia and the Upper Permian of Australia and South Africa.

Comparison. The family is distinguished from Palaeomanteidae and Permembidae by the absence of a long M + CuA, and from Permembidae also in the bifurcation in CuA.

Remarks. For justification of the reconsidered composition and diagnosis of the family, see above (Remarks to the order Palaeomanteida).

Genus *Permosialis* Martynov, 1928

Permosialis: Martynov, 1928, p. 94.

Sarbalopterodes: Storozhenko, 1991, p. 112 (type species *S. frivulus* Storozhenko, 1991) (syn. nov.).

Tologoptera: Storozhenko, 1992b, p. 126 (type species *T. mongolica* Storozhenko, 1992) (syn. nov.).

Type species. *P. paucinervis* Martynov, 1928.

Diagnosis. Wing large, wide (forewing at most 2.5 times as long as wide); forewing almost always with convex anterior margin. SC joining C. RS three-branched. M and CuA connected at base by M_5 or fused for short distance.

Species composition. In addition to the type species and the new species described below, *P. asiatica* O. Martynova, 1961, *P. belmontensis* Riek, 1968, *P. bifasciata* Martynov, 1933, *P. brevifurcata* O. Martynova, 1952, *P. cauleoides* O. Martynova, 1952, *P. defurcata* O. Martynova, 1952, *P. fasciata* O. Martynova, 1952, *P. frivola* (Storozhenko, 1991), *P. immaculata* O. Martynova, 1952, *P. lata* Martynov, 1928, *P. latiformis* O. Martynova, 1952, *P. marmorata* O. Martynova, 1952, *P. matutina* O. Martynova, 1961, *P. mongolica* (Storozhenko, 1992), *P. perfecta* O. Martynova, 1952, *P. quadriramosa* O. Martynova, 1952, *P. sibirica* O. Martynova, 1961, *P. triassica* Novokshonov et Zhuzhgova, 2004, and *P. ualentovae* Novokshonov et Zhuzhgova, 2004 from the Middle Permian of Eurasia (from Russia to Mongolia), the Upper Permian of Australia, and the Middle or Upper Triassic of Kyrgyzstan.

Comparison. The genus in question differs from others in the wide wing and (from all except some *Permonka*) in the three-branched RS; it also differs from *Permonikia* in the SC joining C. In other genera, the wing is much narrower; RS almost always has four or more branches; in *Permonikia*, SC has a terminal bifurcation (joining C and R).

Remarks. The synonymy of *Tologoptera* Storozhenko, 1992 and *Sarbalopterodes* Storozhenko, 1991 reflects the fact that these genera do not differ

from *Permosialis*. For *Tologoptera*, which was originally described in a different order, the differences from *Permosialis* have not been analyzed (Storozhenko, 1992b); for *Sarbalopterodes*, the presence of a number of hairs on the costal vein of both wing pairs was indicated as a distinctive character (Storozhenko and Novokshonov, 1999), but these hairs are hardly visible even precisely in the spot where they are depicted (Storozhenko and Novokshonov, 1999, text-fig. 8), and their presence can hardly be considered to be the main diagnostic character of a genus.

Permosialis zavialovensis Rasnitsyn et Aristov, sp. nov.

Etymology. From Zav'yalovskii District.

Holotype. PIN, no. 3286/124, part and counterpart of incomplete forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 13c, 15b). The forewing has rather small transversely elongate bright dark spots, arranged in transverse rows along not preserved crossveins. The costal space is wide. SC probably has many branches (three, including the apical branch, are in the fragment preserved) and extends beyond the bifurcation of RS. The stem of RS is long. The bifurcations of M and CuA are at the same level, somewhat proximal to the bifurcation of RS. CuP is straight.

Measurements, mm. Length of fragment, 6.4; width, 5.7.

Comparison. The new species differs from congeners in its unusual coloration pattern. It is similar to *P. bifasciata* Martynov, 1933, *P. cauleoides* O. Martynova, 1952, and *P. marmorata* O. Martynova, 1952 in the long stem of RS and differs from it in addition to the coloration pattern in the bifurcations of M and CuA positioned at the same level, while, in *P. bifasciata* and *P. cauleoides*, they are at different levels, and in the straight CuP, while, in *P. marmorata*, CuP is clearly curved (Martynov, 1933; Martynova, 1952).

Material. Holotype.

Permosialis udmurtensis Rasnitsyn et Aristov, sp. nov.

Etymology. From Udmurtia.

Holotype. PIN, no. 3286/123, part and counterpart of incomplete forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 13d, 15c). The forewing has a poorly preserved coloration pattern (possibly, a dark preapical band and an apical spot are present, but they could also represent postburial staining); its apex is distinctly protruding. SC is slightly S-shaped, has four preserved preapical branches, broadly and almost evenly spaced (some basal branches are probably not preserved). RS deviates rather far basally; the length ratio of the stem of RS, the stem of RS_{1+2} , and RS_1 is 1 : 1.4 : 0.7. The stems M and CuA are free or fused within a very short segment; the bifurcation of M is

slightly distal to the bifurcation of RS; the bifurcation of CuA is very slightly more distal. CuP in its preserved portion is straight; 1A has a bifurcation; its stem is straight.

Measurements, mm. Wing length, about 17; width, 7.8.

Comparison. The new species is similar to *P. bifasciata* O. Martynova, 1952 in the ratio between the segments of RS; the latter differs in the short, broadly rounded wing apex, the denser branches of SC, and more distal position of the bifurcation of M (Martynova, 1952).

Permosialis sp.

Description (Fig. 13e). The hindwing lacks a preserved color pattern and has a sequence of bifurcations (CuA, RS, M) unusual for hindwings. SC lacks branches in distal part. The stem of RS₁₊₂ is relatively short.

Measurements, mm. Length of fragment, 20.5; width, 16.0.

Comparison. A similar sequence of bifurcations is only known in *P. frivulus* (Storozhenko, 1991) (Storozhenko and Novokshonov, 1999, text-figs. 5, 6), but it is considerably smaller in size: at the level of the apex of CuA₂, the hindwing is about 10 mm wide, while, in the new species, it is 16 mm wide.

Remarks. The hindwings of *Permosialis* are known insufficiently for reliable identification even based on completely preserved remains. In this case, the sequence of main bifurcations combined with a large size suggest that it is hardly probable that the wing in question belongs to a previously described species.

Material. Specimen PIN, no. 3695/5, impression of forewing fragment; Kostovaty locality, Udmurtia; Urzhumian Stage.

Genus *Epimastax* Martynov, 1928

Epimastax tshepanikha Rasnitsyn et Aristov, sp. nov.

Etymology. From the Chepanikha locality.

Holotype. PIN, no. 3286/125, part and counterpart of forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 13f, 15d). The forewing is darkened (less so distal to the line approximately between the apex of the anal space and the apex of the

anterior branch of RS), with indistinct, rather small, somewhat lighter spots in the basal half of the wing, forming a pattern resembling transverse rows. The pre-radial space is wide, especially within the second quarter of the wing length. SC does not reach one-third of the wing length and has rather infrequent simple branches. R is almost straight and has ten simple anterior branches, a short basal branch deviates near the apical branch of SC. RS diverges very basally, as in the hindwing (it is free already at the level of the basal branch of R), and CuA is rather concave, especially basally, which is also atypical of forewings. However, the characteristic convex clavus, the presence of a typical nodal line, which forms an arch running through the bases of the forks of RS and CuA to the apex of the clavus, as well as the convex anterior wing margin and the wide preradial space confirm that this is a forewing. The first bifurcation of RS is somewhat distal to the bifurcation of CuA; the second bifurcation of RS is in the middle between the first one and the apex of RS₁. The stems of M and CuA are fused to the level of the middle of SC; the bifurcation of M is much more basal than the bifurcation of CuA and even more basal than the first bifurcation of RS. The distances between the branches of M and Cu are subequal (slightly greater than those between the branches of RS). There are four anal veins; they are almost straight (except 1A basally); the anterior ones are more widely spaced than the posterior ones and sometimes have distinct simple, straight crossveins between them (the absence of crossveins in other areas possibly results from the insufficient preservation).

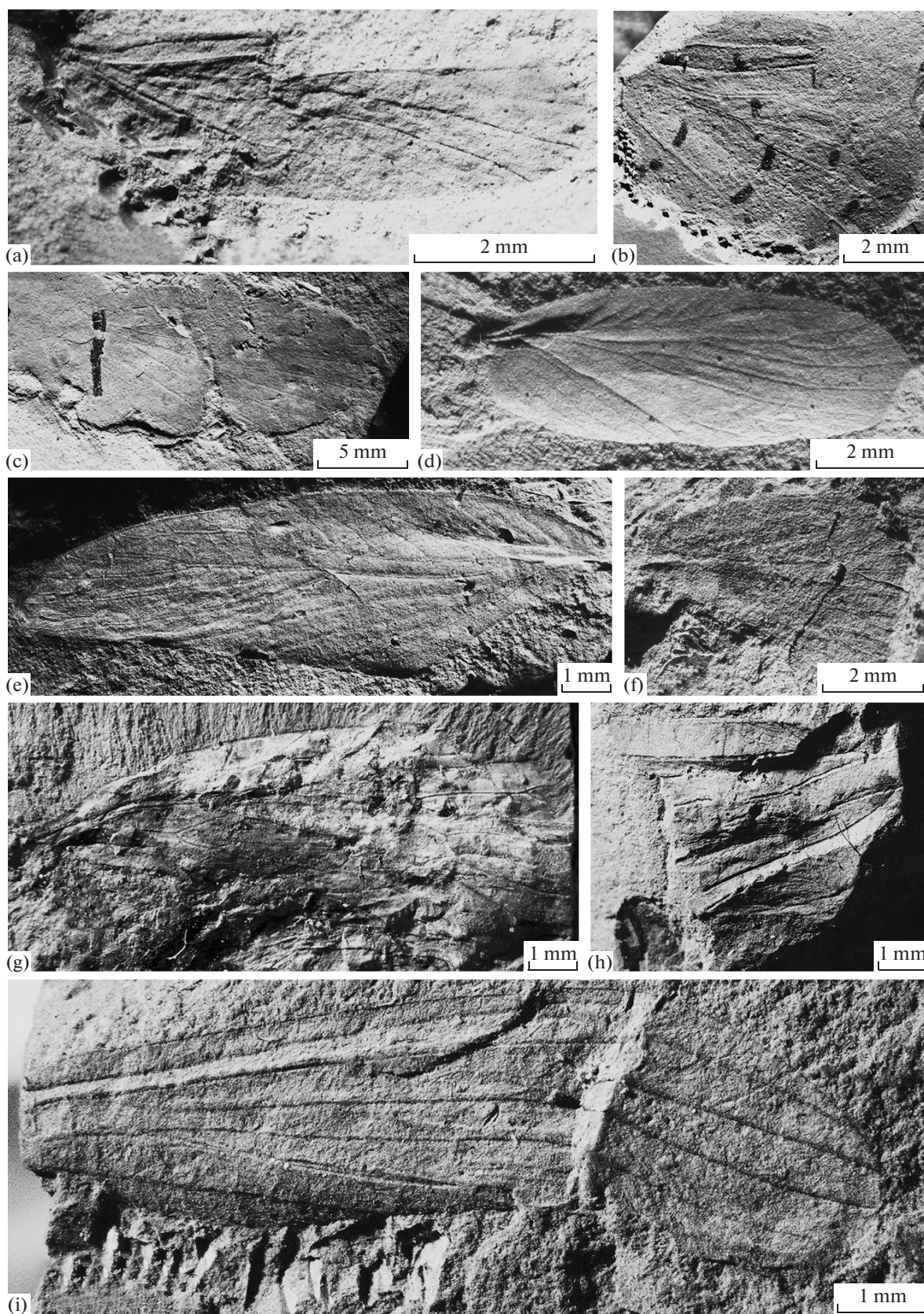
Measurements, mm. Forewing length, 7.8; width, 3.0.

Comparison. The new species is clearly distinguished from congeners by the short SC, the basal position of the base of RS and the bifurcation of M, and in the three-branched RS. In other species of the genus, SC reaches far into the middle one-third of the wing, RS is at least four-branched (unknown in the type species *E. parvulus* Martynov, 1928), and the bifurcation of M is approximately at the level of, or distal to, the bifurcation of RS.

Remarks. The distinguishing characters of the new species are possibly of the generic level.

Material. Holotype.

Fig. 15. Members of the families Palaeomanteidae and Permosialidae (Palaeomanteida): (a) *?Trideloapterum indebitum* sp. nov., holotype PIN, no. 3840/1029, hindwing; Isady locality, Vologda Region; Severodvinian Stage; (b) *Permosialis zavialovensis* sp. nov., holotype PIN, no. 3286/124, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (c) *P. udmurtensis* sp. nov., holotype PIN, no. 3286/123, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (d) *Epimastax tshepanikha* sp. nov., holotype PIN, no. 3286/125, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (e) *E. mutovinensis* sp. nov., holotype PIN, no. 3840/1660, forewing; Isady locality, Vologda Region; Severodvinian Stage; (f) *Balymotikha deterior* sp. nov., holotype PIN, no. 5103/20, forewing; Vyazniki locality, Vladimir Region; Vyatkian Stage; (g) *Onthomastax coprinus* sp. nov., holotype PIN, no. 3286/146, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (h) *Issadembia infracta* sp. nov., holotype PIN, no. 3840/1667, forewing; Isady locality, Vologda Region; Severodvinian Stage; (i) *Neembia ampla* sp. nov., holotype PIN, no. 3840/1670, forewing; Isady locality, Vologda Region; Severodvinian Stage.



Epimastax mutovinensis Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. From the Mutovino locality.

H o l o t y p e. PIN, no. 3840/1660, part and counterpart of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

D e s c r i p t i o n (Figs. 13g–13i; 15e). The forewing lacks preserved traces of coloration. The anterior wing margin is weakly convex. SC is short, reaching at most one-third of the wing length, and has five to eight branches. The preradial space is very wide, probably occupying about one-third of the wing width; R is S-shaped and has 9–12 slightly curved or almost straight branches, the first of which is very long (considerably longer than half the SC length). RS diverges at the level of the bifurcation of M + CuA, bifurcates near the middle of its length, has five branches, and is not always regularly pectinate posteriad: in specimen PIN, no. 3840/559 (Fig. 13i) and, possibly, in specimen PIN, no. 3840/2078 (Fig. 13h), a supernumerary anterior branch of RS is present, reaching the wing margin, probably immediately distal to the apex of R. The stems of M and CuA are short; M is divided approximately at the level of the first quarter of the wing length, between the first and second branches of R; CuA is divided somewhat more distally; thus, the forks are very long. CuP is straight. The anal veins are not preserved. The crossveins are poorly preserved; an individualized long oblique crossvein r-rs is absent.

M e a s u r e m e n t s, mm. Forewing length of holotype, about 13; length of two other forewing fragments, 10 and 7.3 (estimated total wing length is about 11 and 12, respectively).

C o m p a r i s o n. The new species is similar to *E. tshapanikha* sp. nov. and *E. hesterae* Rasnitsyn et Dijk, 2011 from the Normandien Formation of South Africa in the short SC and the proximal deviation of RS (in other congeners, SC reaches far into the second third of the wing length, and RS deviates considerably distal to the first quarter of the wing length); in addition it is similar to *E. hesterae* in the very wide preradial space, very long first branch of SC, and the basal position of the bifurcation of M (in all other species of *Epimastax*, the anterior branch of R is much shorter than half the SC length and M bifurcates near the middle of the wing length). The new species differs from *E. hesterae* in the absence of a strong, long, oblique crossvein 1r-rs, which is typical of this species and the genus *Permonka* Riek, 1973 (Rasnitsyn and Dijk, 2011).

R e m a r k s. The holotype differs from the two other fragments in the considerably longer SC, reaching far beyond the level of the bifurcation of M, and in the absence of the anterior branch of RS; perhaps, these differences are of species rank. However, the incompletely preserved material renders any solution of this question premature. Therefore, the two fragments are tentatively identified as *E. mutovinensis*, but not included in the type series of this species.

The presence of the anterior branch of RS in one or both nontype specimens requires special attention. It is easy to imagine a slight basal shift of this branch, turning it into an individual oblique crossvein r-rs, which is characteristic, as mentioned above, of *E. hesterae* and many species of the genus *Permonka*. Both *Permonka* and *E. hesterae* come from the Normandien Formation, South Africa, presumably somewhat later than that of Isady, but *Permonka* is more typical of the Triassic and Jurassic. The emergence of a supernumerary anterior branch of RS probably models the emergence of the said crossvein and indicates that *Epimastax* is probably closely related to *Permonka*.

M a t e r i a l. In addition to the holotype, specimens PIN, nos. 3840/559 and 3840/2078 from the same locality, not included in the type series.

Genus Balymotikha Rasnitsyn et Aristov, gen. nov.

E t y m o l o g y. From the Balymotikha locality. Gender feminine.

T y p e s p e c i e s. *B. deterior* sp. nov.

D i a g n o s i s. Wing wide, with convex anterior margin. SC long (reaching far beyond second bifurcation of RS), anterior branches undeveloped or weak, position and structure of apex unknown. Anterior branches of R probably undeveloped (possibly except few small terminal branches). RS with at least three branches. Fork of M long (bifurcation almost at level of base of RS); fork of CuA very short. Morphology of anal system unknown.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. The new genus differs from all Permosialidae in the long SC with anterior branches absent or very weak (in *Permosialis*, SC can be long, but with strong anterior branches; in the other genera, SC is shorter) and in the very long fork of M. Additionally, it differs from *Epimastax* and *Permonikia* in the absence of numerous anterior branches of R.

R e m a r k s. The base of M stretching far towards the wing base confirms the assignment of the new genus to the family Permosialidae rather than Palaeomanteidae.

Balymotikha deterior Rasnitsyn et Aristov, sp. nov.

E t y m o l o g y. The Latin *deterior* (inferior).

H o l o t y p e. PIN, no. 5103/20, direct impression of incomplete forewing of mediocre preservation; Balymotikha locality, Vladimir Region; Vyatkian Stage.

D e s c r i p t i o n (Figs. 14a, 15f). The forewing is probably broadly darkened, with many light spots and a dark spot in the interrational, radiomedial, and medio-cubital spaces proximal to the bifurcation of M (the coloration is poorly preserved at the wing base and distal to the dark spot). The anterior wing margin is weakly convex. The preradial space is moderately wide; the costal space is somewhat wider than the sub-

costal space. SC is long, more or less straight, reaching beyond the second bifurcation of RS, probably without anterior branches. RS probably deviates within the basal quarter of the wing; its stem is arcuate; the first two bifurcations are closely set; at least three branches are present. The bifurcation of M is only somewhat distal to the base of RS; the bifurcation of CuA is narrow, at the level of the basal bifurcation of RS, and considerably distal to the bifurcation of M. CuP reaches beyond the level of the bifurcations of RS and CuA.

Measurements, mm. Length of fragment, 6.5; estimated total forewing length, about 11.

Material. Holotype.

Genus *Onthomastax* Rasnitsyn et Aristov, gen. nov.

Etymology. From the Greek *onthos* (dung), referring to the finding of the holotype in a coprolite, and the generic name *Epimastax*. Gender masculine.

Type species. *O. coprinus* sp. nov.

Diagnosis. Wing shape unknown. SC long, terminating into bifurcation. M and CuA fused at one point; fork of M short; fork of CuA extraordinarily long (bifurcation much closer to bifurcation of M and CuA than to base of RS).

Species composition. Type species.

Comparison. The new genus differs from all Palaeomanteida in the extraordinarily long fork of CuA. In the shape of SC it is only similar to *Permonikia*: in the other genera of Permosialidae, SC joins C; in *Epimastax*, in addition, SC is short.

***Onthomastax coprinus* Rasnitsyn et Aristov, sp. nov.**

Etymology. From the latinized Greek *copros* (dung), referring to the finding of the holotype in a coprolite.

Holotype. PIN, no. 3286/146, part and counterpart of crumpled incomplete forewing (without apex and most of anal area) in fish coprolite; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 14b, 15g). The anterior wing margin is moderately convex. The costal and subcostal spaces are subequally moderately wide. SC has short simple branches and terminal branch at the level of the middle of RS between the first and second bifurcations. The base of RS is positioned almost at the middle between the bifurcation of M and CuA and the apex of the posterior branch of SC. RS has at least three branches and a distinct crossvein r-rs at the base of the second bifurcation. M has a broad bifurcation somewhat distal to the first bifurcation of RS. CuA has a short stem; its anterior branch is curved antiad, angulately bent near M, then smoothly curved towards the posterior wing margin; the posterior branch is more or less parallel to the anterior one; both reach the posterior margin slightly distal and slightly proximal, respectively, to the bifurcation of SC. CuP is long, almost reaching the level of the first bifurcation of RS,

with a crossvein cu-a at the level of M + CuA. A dark spot at the posterior wing margin runs from the apex of the distal branch of CuA antiad and towards the wing apex.

Measurements, mm. Length of fragment, 11.3; width, 4.3; estimated total forewing length, 13.

Material. Holotype.

Family Permembriidae Tillyard, 1937

Subfamily Letopalopterinae O. Martynova, 1962

Genus *Issapaloptera* Rasnitsyn et Aristov, gen. nov.

Etymology. From the Isady locality and the generic name *Letopaloptera*. Gender feminine.

Type species. *I. infracta* sp. nov.

Diagnosis. Medium-sized insect. Forewing with medially thickened SC, joining C in distal quarter of wing, not forming bifurcation. RS beginning in basal quarter of wing, free, divided into two branches at proximal boundary of distal one-third of wing. MP two-branched. CuA not forming anastomosis with CuP.

Species composition. Type species.

Comparison. In the presence of SC not forming an apical bifurcation, free RS, and medium size, the new genus is most similar to the genus *Letopaloptera* Martynova, 1961 from the Middle Permian Soyana locality, Arkhangelsk Region, and differs from it in the longer SC. In *Letopaloptera*, SC ends in the basal one-third of the wing (Aristov and Rasnitsyn, 2008).

***Issapaloptera infracta* Rasnitsyn et Aristov, sp. nov.**

Etymology. Feminine gender form of the Latin *infractus* (broken).

Holotype. PIN, no. 3840/1667, impression of slightly distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 14c, 15h). The anterior margin of the forewing is straight. The costal space near the base of RS is 1.6 as wide as the subcostal space. The anterior branches of SC are sparse, simple, straight, weakly inclined. M is divided into MA and MP immediately distal to the base of RS; MA is simple; MP is divided near the middle of the wing. CuA is straight; the intercubital space is somewhat narrower than the medial space. Crossveins are simple, forming a double row of cells in the intermedial space. The wing membrane is light; crossveins are colored.

Measurements, mm. Forewing length, about 11.5.

Material. Holotype.

Genus *Neembia* Rasnitsyn et Aristov, gen. nov.

Etymology. From the generic name *Permembia* Tillyard, 1928. Gender feminine.

Type species. *N. ampla* sp. nov.

Diagnosis. Width of preradial space in basal one-third of wing more than one-fourth of wing width. SC with long, S-shaped, widely spaced, anterior branches. RS beginning at level of divergence of M and CuA. M divided into MA and MP considerably distal to base of RS.

Species composition. Type species.

Comparison. In the wide preradial space, *Neembia* is similar to *Visherifera* Novokshonov, Ivanov et Aristov, 2002 from the Kungurian and Ufimian of the Perm Region and differs from it in the proximal position of the base of RS. In *Visherifera*, RS begins near the middle of the wing, considerably distal to the point of divergence of M and CuA. In the RS beginning close to the level of divergence of M and CuA, the new genus is similar to *Permambia* from Leonardian deposits of Kansas, United States, and differs from it in the wide costal space, which in the latter genus is less than 20% of the wing width (Aristov and Rasnitsyn, 2008).

Neembia ampla Rasnitsyn et Aristov, sp. nov.

Etymology. Feminine gender form of the Latin *amplus* (large).

Holotype. PIN, no. 3840/1670, impression of distorted forewing fragment; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 14d, 15i). The anterior margin of the forewing is straight. RS is simple up to the middle of the wing. CuA is straight; the intercubital space is narrower than the medial space. Crossveins are simple. The wing membrane of is light; crossveins are colored.

Measurements, mm. Forewing width, 5.5; estimated length (calculated from the average ratio of wing length and width in Permambiidae, 3.4), about 19.

Material. Holotype.

Order Jurinida M. Zalesky, 1929

Remarks. The order Jurinida, or Glosselytroidea, is a rather small group of insects, which existed from the Early Permian to the mid-Jurassic. The peculiar wing morphology long prevented the recognition that they were neuropteroids (Sharov, 1966; Rohdendorf and Rasnitsyn, 1980). The system of the order at the family level was excessively subdivided, and serious problems remained even after the reduction of the number of families from seven to three (Rasnitsyn and Quicke, 2002). These problems are partially related to the fact that the system was previously based on the morphology of the precostal area, rather rarely preserved in fossils. The necessity to describe new Jurinida from the Upper Permian of Russia compels us to reconsider the system of the order once again.

The archaic family Permoberothidae from the Lower Permian of the United States, which differs from others in the forewing lacking a precostal area and ambient veins and in the retention of a long SC of

ordinary appearance, is clearly distinguished from the other Jurinida and is not analyzed hereinafter. The fossils grouped into the families Jurinidae and Polycytellidae (sensu Rasnitsyn and Quicke, 2002) are characterized by a peculiar morphology of the forewing. It is more or less symmetrical relative to the longitudinal axis (Figs. 16, 17a, 17b, 18a), with lanceolate precostal and anal lobes often similar in size and shape (in Fig. 17b, the anal lobe is incomplete or secondarily diminished). SC is shortened almost to the apex of the precostal area. One or, more often, two ambient veins (parallel to the wing margin) are recognized: R and CuP; usually (and, judging from Permoberothidae, primarily) two individual parallel veins run along the wing axis. Judging from the hindwing of *Permoberotha* Tillyard, 1932, these veins are homologous to the posterior branch of RS and the anterior branch of M (Rasnitsyn and Quicke, 2002). They are more or less closely set (sometimes very closely) or even fused and, in contrast to the remaining part of the wing, lack or almost lack crossveins between them. In some cases (*Glosselytron martynovae* Ponomarenko, 1988, *G. linguale* Ponomarenko, 1988, *Ladinoglosselytron martynovae* Hong, 2007), evident traces of fusion between parallel veins are discernible. Sometimes (in *Uskatelytron* O. Martynova, 1952), all veins extending along the wing axis are more or less identical.

Parallel veins fused into a single axial vein, along with two ambient veins joined at the wing apex, constituted the diagnostic character of the family Polycytellidae. The presence of a transitory state, with parallel veins almost, but not entirely fused into a single axial vein in the above-mentioned species, compromises the former separate status of this family. An even greater problem is the fact that it was no coincidence that *Glosselytron martynovae* and *G. linguale* were assigned to the genus *Glosselytron*, the type species of which has two parallel veins; in a number of other characters they are actually similar to *G. multivenosum* Martynov, 1938. By contrast, *Ladinoglosselytron martynovae* is close to other Triassic species from China (see above) and, along with them, forms a group of species allied to other Mesozoic Jurinida, representing the genus *Mesojurina* O. Martynova, 1943. Via *L. martynovae*, all of them are close to *Jurina* and *Eoglosselytrum*, which retain paired parallel veins. At the same time, all species with fused or almost fused parallel veins also have a single ambient vein along the entire wing margin (sometimes with a small gap at the very apex of the wing), while, in species with two widely set parallel veins, the ambient veins are interrupted at the apex of the wing and, in *Glosselytron*, the posterior ambient vein is simply absent.

Thus, the correlated pair of characters, namely, the complete or almost complete ambient vein and the single axial vein (with traces of the initial paired state or without such traces) probably evolved independently in two Jurinida lineages: in the *Jurina*-like ancestor of Mesozoic *Mesojurina*, *Ladinoglosselytron*, etc. and in the ancestor close to *Glosselytron* of "*G.*" *martynovae*,

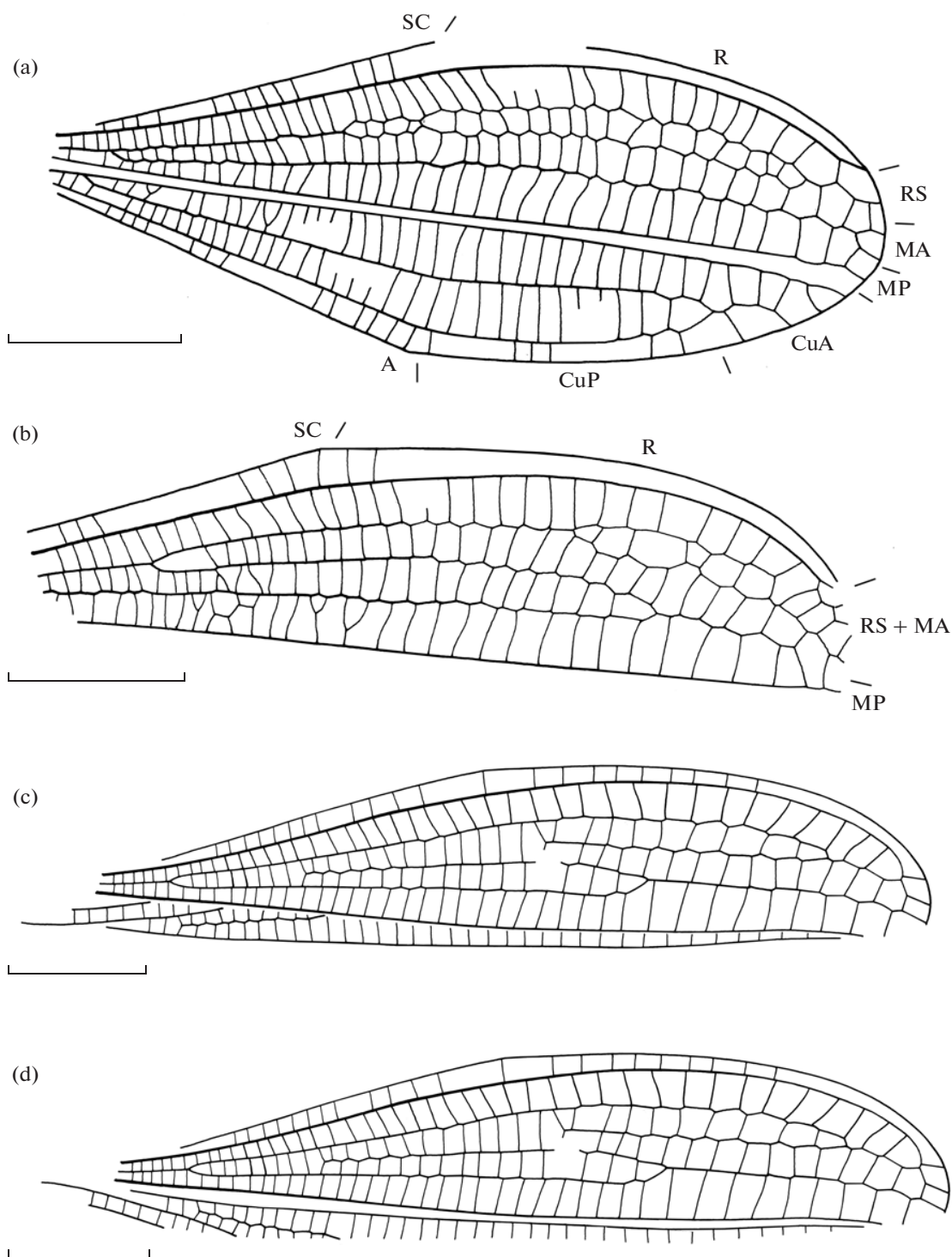


Fig. 16. *Eoglosselytrum biarmicum* sp. nov. (Jurinida: Jurinidae), forewings; Chepanikha locality, Udmurtia; Urzhumian Stage: (a) holotype PIN, no. 3286/120; (b) paratype PIN, no. 3286/121; (c, d) paratype PIN, no. 3286/138: (c) preserved venation; (d) reconstruction.

"G." linguale, *Polycytella*, etc. Therefore, we are compelled to reject opposing Polycyttellidae to other Jurinida and return to the question about the system of the order.

First of all, let us put aside archaic Permoberothidae, the separate status of which is doubtless (see above), and *Archoglossopterum* O. Martynova, 1958, another peculiar genus characterized by gener-

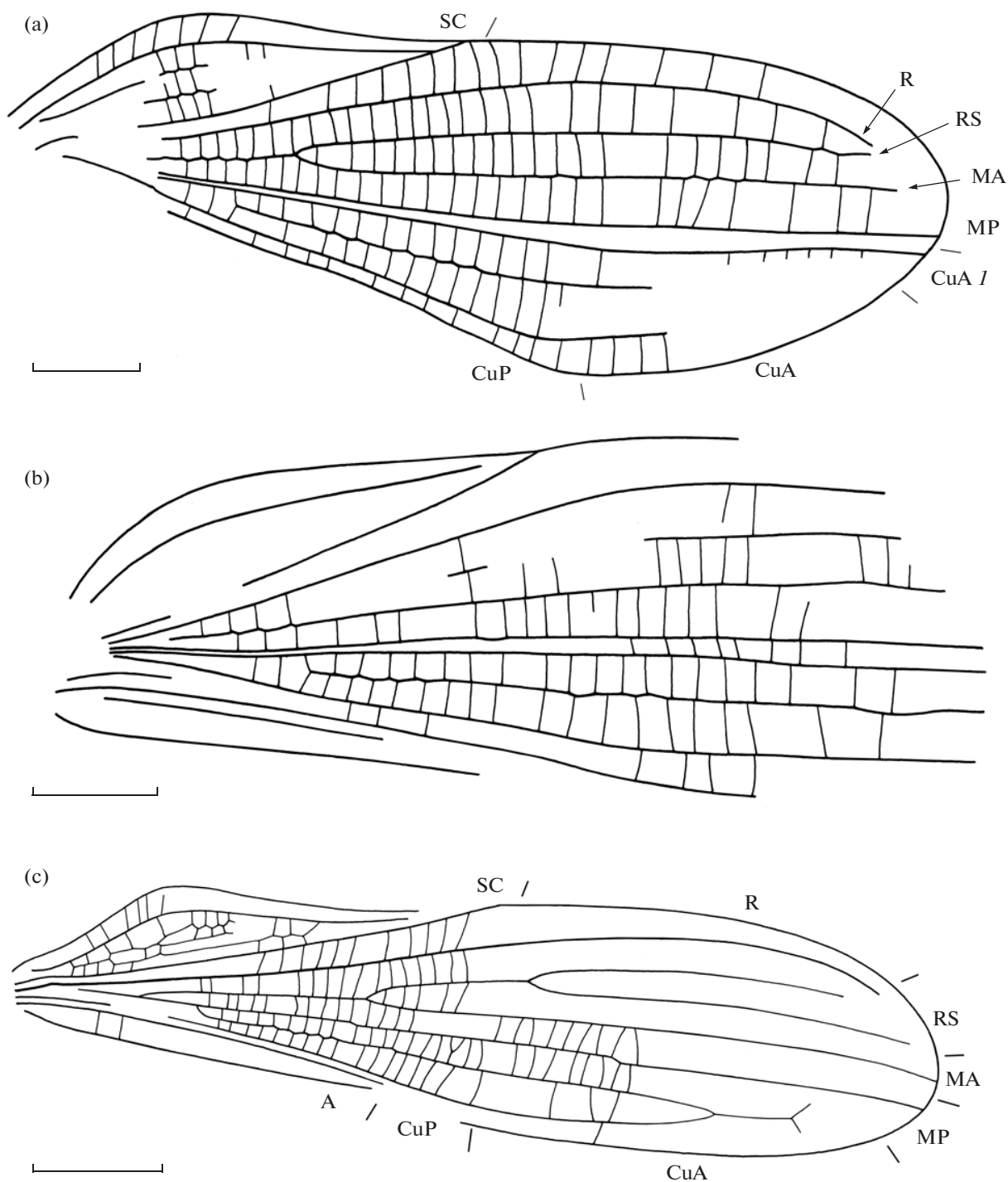


Fig. 17. Members of the family Jurinidae (Jurinida), forewings: (a, b) *?Eoglosselytrum kultshumovense* sp. nov., Kul'chumovo locality, Orenburg Region; Severodvinian Stage: (a) holotype PIN, no. 5273/26; (b) paratype PIN, no. 5273/25; (c) *Isadelytron speciosum* sp. nov., holotype PIN, no. 3840/443, Isady locality, Vologda Region; Severodvinian Stage.

ally infrequent veins, widely set parallel veins, only two rows of cells in the precostal space, and a relatively wide space between the bases of RS and M + CuA in the wing base. This is probably the second early branch

of the order, which should retain family rank as Archoglossopteridae O. Martynova, 1958.

Among the bulk of remaining Jurinida, the type genus *Jurina* M. Zalesky, 1929, judging from the bet-

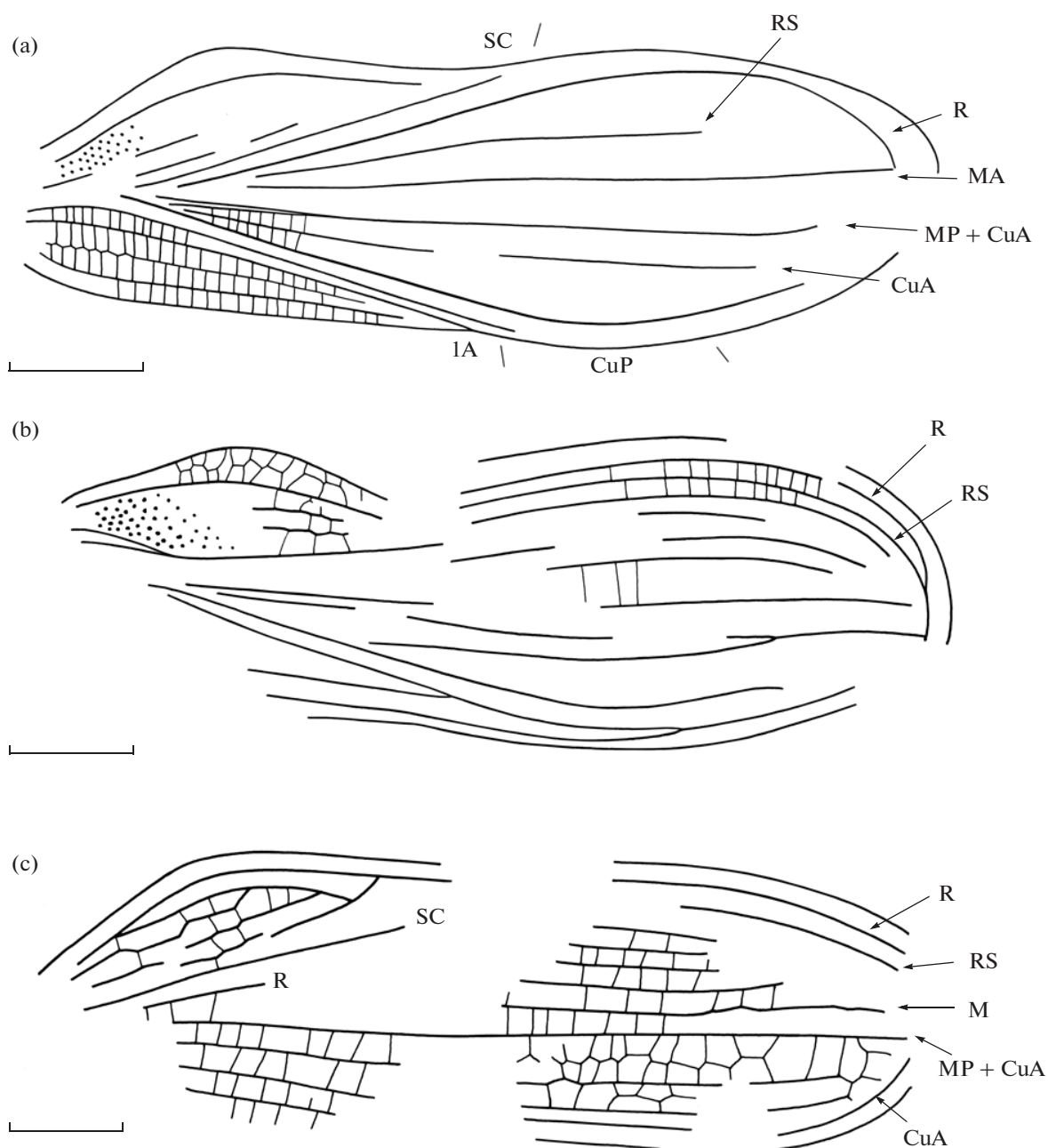


Fig. 18. Members of the families Jurinidae and Glosselytridae (Jurinida), forewings: (a, b) *?Isadelytron planum* sp. nov.; Chepanikha locality, Udmurtia; Urzhumian Stage: (a) holotype PIN, no. 3286/136; (b) paratype PIN, no. 3286/137; (c) *?Karajurina desperata* sp. nov., holotype PIN, no. 3840/398; Isady locality, Vologda Region; Severodvinian Stage.

ter known species *J. marginata* Martynov, 1938 (the type species was poorly described and the material was probably lost), is clearly close to *Eoglosselytrum* O. Martynova, 1952, *Protojurina* O. Martynova, 1958, and *Surijoka* O. Martynova, 1958, which differ mostly in the density and regularity of the pattern of crossveins, with the accumulation of material making dis-

tinguishing between them more and more difficult. These four genera share the following characters: ambient veins are clearly pronounced, but far from joining at the wing apex; parallel veins are distinctly closely set, but not fused and lacking crossveins between them; and the number of longitudinal veins is relatively small (usually no more than seven, rarely,

eight rows of cells across the wing in its middle portion between the ambient veins, excluding the space between the closely set axial veins).

The center of the other group, in a sense alternative, is formed by *Glosselytron* Martynov, 1938 and *Glossopterum* Sharov, 1966, which are characterized, in addition to a pair of closely set parallel (axial) veins, like in the previous group, by only one, anterior ambient vein and a greater number of longitudinal veins and at least ten rows of cells behind the anterior ambient vein across the wing in its middle portion.

The Jurinida displaying a trend towards the elytrization of venation are more or less close to the two groups recognized above. This trend is realized partially by strengthening the membrane, as in most elytropterous insects, and partially by the thickening of veins, as in beetles. The former process prevails among oligoneurous forms, mostly Triassic (*Mesojurina* O. Martynova, 1943 and its possible synonyms *Shaanxiglosselytron* Hong, 2007 and *Sinoglosselytron* Hong, 2007); the latter is prevails in more polyneurous Permian and Triassic genera (*Polycytella* Tillyard, 1922, *Mongoljurina* Ponomarenko, 1988, *Karajurina* Vilesov et Novokshonov, *Uskatelytron* O. Martynova, 1952, and *Argentinoglosselytrina* Martins-Neto et al., 2003), but, in both cases, the anterior and posterior ambient veins join at the wing apex and the two axial veins are fused (sometimes incompletely) into one. The last vein in some cases (in *Uskatelytron* and *Argentinoglosselytrina*) loses its individuality. The affinity of "*Glosselytron*" *martynovae*, "*Glosselytron*" *linguale*, and the true *Glosselytron*, with its nonelytrized wing, lacking the posterior ambient vein and a trend towards the fusion of axial veins, is quite obvious. On the other hand, evident similarity is also displayed by *Jurina*, related oligoneurous *Mesojurina* and their analogues (synonyms?) from China.

In the light of the above-said, we can provisionally accept the hypothesis that the differentiation of Permoberothidae and Archoglossopteridae from the common stem of the order Jurinida was followed by divergence into the oligoneurous and polyneurous lineages. The former lineage, with early development of the posterior ambient vein, in the course of the subsequent elytrization, mostly strengthened the wing membrane; the latter lineage acquired the posterior ambient vein more or less simultaneously with elytrization, which was largely realized by the thickening of veins. We regard the oligoneurous lineage as the family Jurinidae M. Zalesky, 1929, comprising of *Jurina* M. Zalesky, 1929, *Eoglosselytrum* O. Martynova, 1952, *Protojurina* O. Martynova, 1958, *Surijoka* O. Martynova, 1958, *Mesojurina* O. Martynova, 1943, *Shaanxiglosselytron* Hong, 2007, *Sinoglosselytron* Hong, 2007 (the separate status of these genera, especially the last three, is not entirely doubtless), and a new genus, transitional between Permian and Mesozoic forms (see below).

The polyneurous lineage, comprising *Glosselytron* Martynov, 1938, *Glossopterum* Sharov, 1966, *Uskatelytron* O. Martynova, 1952, and *Mongoljurina* Ponomarenko, 1988 (including *M. martynovae* (Ponomarenko 1988) comb. nov. and *M. linguale* (Ponomarenko, 1988) comb. nov.), *Karajurina* Vilesov et Novokshonov, 1994, and *Sinojurina permiana* Huang et al., 2007, is regarded as the family Glosselytridae Martynov, 1938.

Family Jurinidae M. Zalesky, 1929

Jurinidae: M. Zalesky, 1929, p. 28.

Anorthoneuridae: Martynov, 1938b, p. 197 (type genus *Anorthoneura* Martynov, 1938 = *Jurina* M. Zalesky, 1929).

Eoglosselytridae: Martynova, 1952, p. 191 (type genus *Eoglosselytrum* O. Martynova, 1952).

Type genus. *Jurina* M. Zalesky, 1929.

Diagnosis. Precostal lobe in forewing distinct, with ambient vein rather often separating dilated border and with several mostly horizontal veins. Main portion of wing with both ambient veins (R and CuP) distinct, joining or not joining at wing apex and with parallel axial veins (posterior branch of RS and anterior branch of M) clearly closely set or fused partially or completely. Base of wing disc narrow (squeezed between precostal and anal lobes) and filled with stems of RS, M, and CuA, without visible free space left. Middle portion of wing with at most eight rows of cells across disc between ambient veins. Elytrization realized mostly by thickening of membrane.

Generic composition. In addition to the type genus *Eoglosselytrum* O. Martynova, 1952, *Protojurina* O. Martynova, 1958, *Surijoka* O. Martynova, 1958, and a new genus from the Middle and Late Permian of Eurasia and Australia; *Mesojurina* O. Martynova, 1943, *Ladinoglosselytron* Hong, 2007, *Shaanxiglosselytron* Hong, 2007, *Sinoglosselytron* Hong, 2007 from the Upper Triassic and Lower Jurassic of Central Asia and China.

Comparison. The family considered differs from Permoberothidae in the presence of the precostal lobe and ambient veins; it differs from Archoglossopteridae in the closely set or fused axial veins, more polyneurous precostal area, and the absence of significant free space at the wing base; it differs from Glosselytridae in the presence of posterior ambient vein and/or the more depleted venation of the disc (at most eight rows of cells across the wing between ambient veins).

Genus *Eoglosselytrum* O. Martynova, 1952

Eoglosselytrum: Martynova, 1952, p. 191.

Type species. *E. kondomense* O. Martynova, 1952.

Diagnosis. Ambient veins not joining at wing apex; parallel (axial) veins closely set, but not fused. Longitudinal veins on disc partly zigzagging, many cells on disc markedly less than two times higher than

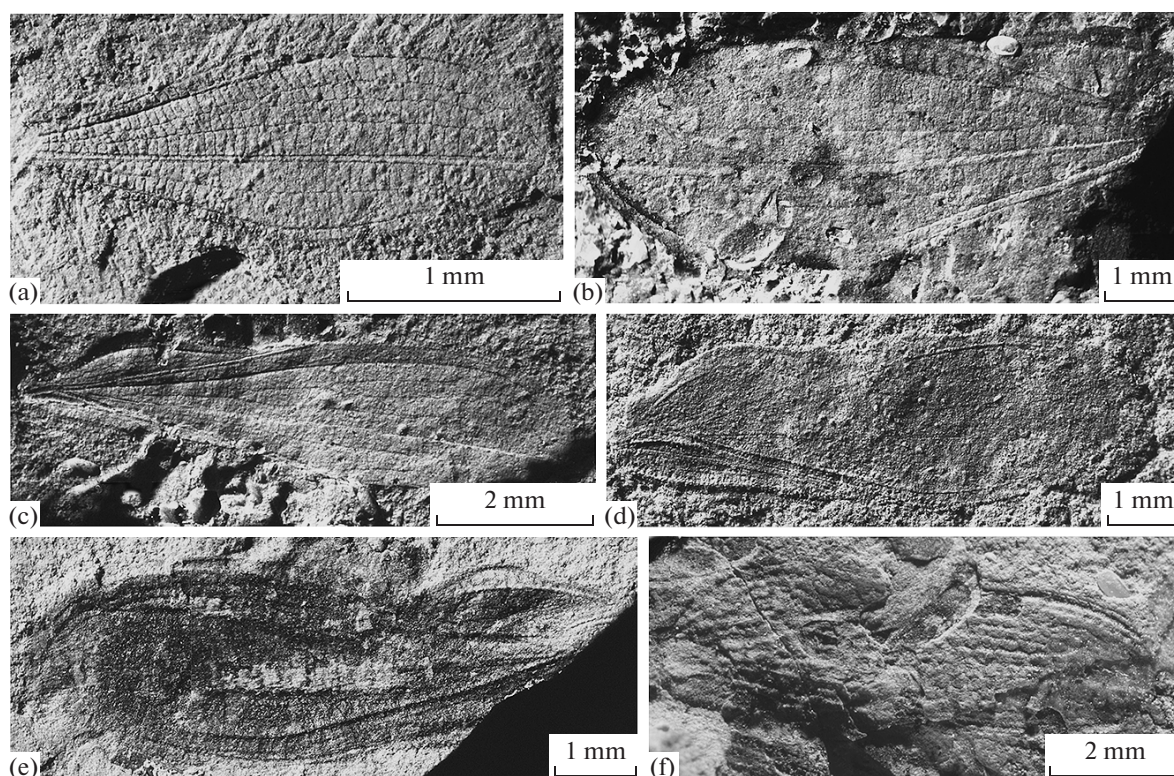


Fig. 19. Members of the families Jurinidae and Glosselytridae (Jurinida), forewings: (a) *Eoglosselytrum biarmicum* sp. nov., holotype PIN, no. 3286/120, Chepanikha locality, Udmurtia; Urzhumian Stage; (b) *?Eoglosselytrum kultshumovense* sp. nov., holotype PIN, no. 5273/26, Kul'chumovo locality, Orenburg Region; Severodvinian Stage; (c) *Isadelytron speciosum* sp. nov., holotype PIN, no. 3840/443, Isady locality, Vologda Region; Severodvinian Stage; (d, e) *?Isadelytron planum* sp. nov.; Chepanikha locality, Udmurtia; Urzhumian Stage: (d) holotype PIN, no. 3286/136; (e) paratype PIN, no. 3286/137; (f) *?Karajurina desperata* sp. nov., holotype PIN, no. 3840/398; Isady locality, Vologda Region; Severodvinian Stage.

wide. Anteriorly, considerably more than 16 cells per row along axial veins. Border of precostal space wide, especially medially.

Species composition. In addition to the type species, *E. anomale* O. Martynova, 1961, *E. kaltanicum* O. Martynova, 1952, *E. kuznetzkiense* O. Martynova, 1952, *E. perfectum* O. Martynova, 1961, *E. pictum* O. Martynova, 1961, *E. sharovi* O. Martynova, 1961, and *E. usinskiense* O. Martynova, 1961 from the Middle Permian of the Kuznetsk Basin; *E. zalesskyi* Vilesov et Novokshonov, 1994 from the Upper Permian of Kazakhstan; *E. perplexum* (Riek, 1953) from the Upper Permian of Australia; and a new species from the Middle Permian of Udmurtia.

Comparison. The nonfused axial veins and nonjoining ambient veins make this genus similar to *Jurina*, *Protojurina*, and *Surijoka*, among which the last is especially close to it in the partially zigzagging longitudinal veins and not always high cells. *Eoglosselytrum* differs from *Surijoka* in the smaller cells and, thus, longer longitudinal rows of them.

Eoglosselytrum biarmicum Rasnitsyn et Aristov, sp. nov.

Etymology. From the Biarmian Series of the Permian.

Holotype. PIN, no. 3286/120, part and counterpart of incomplete forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 16, 19a). In front of parallel veins, branches of RS at the wing base are partially straight; more distally, they are zigzagging. Cells in the rows adjacent to the ambient and parallel veins are high, columnar. Most of the cells in the intermediate rows (in the anterior half of the wing) are less than two times higher than wide.

Measurements, mm. Holotype: length of forewing impression, 6.1; width, 2.2; paratypes PIN, nos. 3286/121 and 138: length of impression, 6.2 and 6.4, respectively.

Comparison. The new species is distinguished by the presence of straight veins between the parallel and ambient veins at the base of the wing (in the other species, veins in this area are zigzagging); it also differs from most of congeners in the high cells in rows adjacent to the parallel and ambient veins (in the other

species, except the type species, most cells in these rows are lower).

Material. In addition to the holotype, paratypes PIN, nos. 3286/121 and 138 from the same locality.

?Eoglosselytrum kultshumovense Rasnitsyn et Aristov, sp. nov.

Etymology. From the Kul'chumovo locality.

Holotype. PIN, no. 5273/26; part and counterpart of almost complete forewing (without anal area) of satisfactory preservation; Orenburg Region, Saraktashskii District, right bank of the Sakmara River, second gully 3 km downstream from the village of Kul'chumovo; Upper Permian, Severodvinian Stage.

Description (Figs. 17a, 17b, 19b). The precostal space has a border dilated moderately medially; three rows of cells are present in this space behind the border. The disc between the ambient veins has three rows of cells in front of the axial veins and two rows behind them; the cells are relatively high, often two times higher than wide; the veins are weakly zigzagging. The anal space (partially preserved in the paratype) is probably narrow.

Measurements, mm. Holotype: length of forewing impression, 8.8; width, 3.1; paratype: length of impression, 7.2; estimated wing length, about 9; width, at least 2.8.

Comparison. The new species differs from the others in the large size, the weakly zigzagging veins on the disc, and, except for the type species, in the higher cells; it also differs from those species in which this character is known in the weak medial dilation of the border of the precostal space and in the narrow anal area. In the other species of *Eoglosselytrum*, the forewing was indicated to be at most 6 mm long, the majority of cells on the disc are almost always less than twice higher than wide, the border of the precostal space is dilated sharply medially, and the anal space is wider.

Remarks. The characters distinguishing the new species from congeners make it similar to *Jurina*, although this similarity is not so close to assign it to this genus, but it is sufficiently close to raise the question of whether or not the two genera are separate. However, because of the incomplete preservation of specimens this question remains unsolved.

Material. In addition to the holotype, paratype PIN, no. 5273/25 from the same locality.

Genus *Isadelytron* Rasnitsyn et Aristov, gen. nov.

Etymology. From the Isady locality and the generic name *Glosselytron*. Gender neutral.

Type species. *I. speciosum* sp. nov.

Diagnosis. Precostal space with wide, strongly medially dilated border, with weak longitudinal veins. Ambient veins terminating far short of reaching wing apex and not joining. Parallel veins fused seamlessly. Longitudinal veins on disc partially zigzagging. Six rows of cells varying in shape (from high to almost

square) present medially across wing between ambient veins.

Species composition. Two new species described below.

Comparison. In the general venation pattern, including the shape of the precostal space, the new genus is similar to *Eoglosselytrum*, which is probably ancestral to it; however, the new genus is clearly distinguished from *Eoglosselytrum* and similar to *Mesojurina* and other Mesozoic oligoneurous Jurinida in the parallel veins completely fused into a single axial vein. Thus, the new genus models a transitional form between Permian and Mesozoic genera of Jurinida.

Isadelytron speciosum Rasnitsyn et Aristov, sp. nov.

Etymology. Neutral form of the Latin *speciosus* (beautiful).

Holotype. PIN, no. 3840/443, part and counterpart of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 17c, 19c). The wing is narrow, uncolored. The precostal space contains three weak veins in the posterior comb, which disappear proximally and distally in the network. RS is smooth (not zigzagging), three-branched in the posterior comb, diverging from the axial vein. MP + CuA is simple, diverges from the axial vein, partially zigzagging near the base, and joins the posterior ambient vein (CuP) in the distal quarter of the wing. Two preserved anal veins are smooth, weakly curved, form a narrowly lanceolate cell almost as long as the precostal space. Crossveins are simple, less often Y-shaped; cells are usually 1.5–2 times higher than wide.

Measurements, mm. Forewing length, 9.0; width, 2.2.

Material. Holotype.

?Isadelytron planum Rasnitsyn et Aristov, sp. nov.

Etymology. Neutral form of the Latin *planus* (flat).

Holotype. PIN, no. 3286/136, part and counterpart of complete forewing of mediocre preservation (impression flattened, except the anal area, devoid of organic substances, and almost devoid of relief, so that venation is very poorly visible); Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 18a, 18b, 19d, 19e). The wing (both the disc and the precostal and anal spaces) is relatively wide. The precostal space in the basal half is sclerotized, with tuberculate sculpture; more distally, it has weak longitudinal veins, separating three rows of cells. The border of the precostal space is dilated medially and contains two rows of cells. The ambient veins terminate far short of reaching the wing apex. The axial veins are set very closely basally, then, fused, with only two veins between them and the anterior ambient vein and a single vein between them and

the posterior ambient vein. The axial and preceding veins (RS + M and the posterior free RS) reach the wing apex. RS + M and RS diverge close to the disc base. The veins on the disc are not obviously zigzagging. The cells on the disc are poorly preserved; many or all of them were probably narrow and high. The anal space contains four distinct veins (3A is finer than the others and partially zigzagging).

Measurements, mm. Forewing length, 6.7 (holotype) to 7; width, 2.2.

Comparison. The new species is clearly distinguished from the type species in the wider and shorter wing, two rows of cells in the precostal border, and only two veins between the anterior ambient vein and the axial vein.

Remarks. The precostal space with tuberculate basal sculpture and two rows of cells in the border distinguishes the new species from all other Jurinida. These features suggest that the new species probably represent a separate genus, but the poor preservation of both known specimens compels us to postpone formal establishment of this genus, until additional fossil material becomes available.

Material. In addition to the holotype, paratype PIN, no. 3286/137 from the same locality (four overlapping wings, preventing a detailed reconstruction of venation; however, the similarity in general shape, size, and preserved details of venation and, particularly, similar structure of the precostal space strongly suggest that the holotype and paratype are conspecific).

Family Glosselytridae Martynov, 1938

Glosselytridae: Martynov, 1938b, p. 204.

Polycyttellidae: Martynova, 1952, p. 189 (type genus *Polycyttella* Tillyard, 1922).

Uskatelytridae: Martynova, 1952, p. 190 (type genus *Uskatelytron* O. Martynova, 1952).

Glossopteridae: Sharov, 1966, p. 85 (type genus *Glossopterum* Sharov, 1966).

Type genus. *Glosselytron* Martynov, 1938.

Diagnosis. Forewing with distinct precostal lobe, sometimes with elements of flabellate venation, with ambient vein (sometimes not entirely distinct), but without wide border. Most of wing only with anterior ambient vein (R), or with two such veins (R and CuP), but more narrowly joining at wing apex, and with parallel axial veins (posterior branch of RS and anterior branch of M) clearly closely set or partially or entirely fused. Base of disc narrow (squeezed between precostal and anal lobes) and filled with stems of RS, M, and CuA, without visible free space. Middle portion of wing with at least ten rows of cells across disc behind anterior ambient vein. As forewing elytrized, thickening primarily involving membrane.

Generic composition. In addition to the type genus, *Polycyttella* Tillyard, 1922 from the Upper Triassic of Australia; *Argentinoglosselytrina* Martins-Neto et Gallega, 2001 from the Triassic of Argentina; *Glosselytron* Martynov, 1938, *Uskatelytron* O. Martynova,

1952, *Glossopterum* Sharov, 1966, *Karajurina* Vilesov et Novokshonov, 1994, *Mongolajurina* Ponomarenko, 1988, and *Sinojurina* Huang et al., 2007 from the Permian of northern Eurasia.

Comparison. The family differs from Permoberothidae in the presence of the precostal lobe and anterior or anterior and posterior ambient veins; it differs from Archoglossopteridae in the closely set or fused axial veins, more polyneurous precostal area, and the absence of significant free space at the wing base; it differs from Jurinidae in the richer venation of the disc (at least 10 rows of cells behind the anterior ambient vein) and often in the absence of the posterior ambient vein.

Genus *Karajurina* Vilesov et Novokshonov, 1994

Type species. *K. unica* Vilesov et Novokshonov, 1994.

Diagnosis. Only distal half of forewing known, almost without precostal and anal lobes. Ambient veins joining at wing apex. Axial vein single, distinct; about ten rows of uniform, roughly isometric cells present across wing between ambient veins.

Species composition. In addition to the type species, probably another species, described below.

Comparison. The genus differs from all others with a closed ambient vein (all genera except *Glosselytron* and *Glossopterum*) in the oligoneurous wing (ten rows of cells between the ambient veins).

?*Karajurina desperata* Rasnitsyn et Aristov, sp. nov.

Etymology. Feminine gender form of the Latin *desperatus* (hopeless).

Holotype. PIN, no. 3840/398, part and counterpart of incomplete hindwing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 18c, 19f). The forewing is darkened (details of the coloration are unclear because of the poor preservation), elytrized (the veins are noticeably thickened; the shape of the veins and cells is hardly discernible), almost parallel-sided, with symmetrically rounded ends; the precostal space is not protruding. The ambient veins are probably joined; the axial vein is single; 10–11 rows of cells are present across the wing between the ambient veins (seven in front of the axial vein and three or four behind it). Four weak subhorizontal veins are present in the precostal space behind the ambient vein; the border is distinct, narrow.

Measurements, mm. Forewing length, 7.3; width, 2.3.

Comparison. The new species differs from *K. unica* Vilesov et Novokshonov, 1994 in the much more strongly pronounced longitudinal veins on the disc inside the ambient vein; in the type species, this space is occupied almost completely by a network of veins, the axial vein is lost in the network near the

apex, and the other longitudinal veins are barely individualized. Additionally, in the type species, five rows of cells are present at the widest point of the wing in front of the axial vein and behind the ambient vein, while the new species has seven rows of cells.

Remarks. The species is tentatively assigned to the genus *Karajurina* because of the insufficient preservation of the holotype and considerable differences in the strength of longitudinal veins.

Material. Holotype.

2.2. The Latest Member of the Order Mischopterida = Megasecoptera (Insecta) from the Upper Permian Isady Locality

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In this chapter, a new genus and species, *Issadohymen ponomarenkoi* gen. et sp. nov. from the Severodvinian Isady locality, Vologda Region, is described in the family Moravohymenidae, suborder Mischopterina, order Mischopterida.

In the Isady locality (see Chapter 1.2), one wing fragment representing the suborder Mischopterina Handlirsch, 1906 of the order Mischopterida Handlirsch, 1906 has been found. The order is known mainly from the Upper Carboniferous and Lower Permian; its members have a worldwide distribution. Mischopterina is one of the most diverse suborders, comprising 11 families, which occur from the Upper Carboniferous to Lower Permian. In the Late Carboniferous, Mischopterina occurred in North America, Europe, and Siberia; in the Early Permian, they became less diverse, but remained the dominant group among Mischopterida. Their geographical distribution at that time was limited to Europe (Sinitshenkova, 2002). In Russia, only one family has been found, Vorkutiidae Rohdendorf, 1947, which includes two monotypic genera, *Vorkutia* Rohdendorf, 1947 from the Lower Permian of the Vorkuta Basin and *Siberiohymen* Rohdendorf, 1961 from the Upper Carboniferous of the Kuznetsk Basin; both were described from wing fragments lacking basal and cubital parts (Rohdendorf et al., 1961). This family has apomorphic characters, such as the well-developed costalization of the wing, which manifests itself in the strengthened costa and radius, and the shortened subcosta.

The wing from Isady was assigned to the family Moravohymenidae Kukalova-Peck, 1972, established for a single monotypic genus, *Moravohymen* Kukalova-Peck, 1972, described from the Lower Permian of Moravia (Kukalova-Peck, 1972). This family displays some plesiomorphic characters; it has a wide, weakly costalized wing with many longitudinal veins

and few crossveins, which are not arranged in regular rows.

All hitherto known members of the order Mischopterida come from earlier deposits than those of Isady. The genus *Karohymen* Riek, 1976, described from the Upper Permian Mooi River locality (Normandien Formation, South Africa; see Chapter 3.1), was erroneously referred to this order (Dijk and Geertsema, 1999). In fact, it belongs to Diaphanopterida, because its wing has MA and RS distinctly joining near their bases, which is characteristic of diaphanopterids.

Although the new genus *Issadohymen* gen. nov. is the latest known member of the order, its wing has even more primitive characters than that of *Moravohymen*. Its very broad costal space with many crossveins, long subcostal vein almost reaching the wing apex, and crossveins in the pterostigmal area of the wing are evidence of a primitive state of the wing shape and venation in *Issadohymen* gen. nov.

Order Mischopterida Handlirsch, 1906

Suborder Mischopterina Handlirsch, 1906

Family Moravohymenidae Kukalova-Peck, 1972

Genus *Issadohymen* Sinitshenkova et Aristov, gen. nov.

Etymology. From the Isady locality and the Greek *hymen* (wedding song).

Type species. *Issadohymen ponomarenkoi* sp. nov.

Diagnosis. Costal space wide, with many crossveins; SC long, almost reaching wing apex and joining C, connected with it by short crossveins in pterostigmal area. R reaching wing apex; RS with five branches, its anterior branch divided. M branching distal to first bifurcation of RS; CuA and CuP simple. Crossveins simple, rather few and not regular.

Species composition. Type species.

Comparison. The new genus is clearly distinguished from *Moravohymen* in the greater number of branches of RS, more distal branching of M, and longer SC. *Moravohymen* has four branches of RS, M branching considerably basal to the first bifurcation of RS, and SC terminates short of reaching the wing apex (Kukalova-Peck, 1972).

Issadohymen ponomarenkoi Sinitshenkova et Aristov, sp. nov.

Etymology. In honor of the distinguished paleontologist A.G. Ponomarenko.

Holotype. PIN, no. 3840/799, part and counterpart of wing fragment without basal and cubital portions; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 20a, 20b). The preserved part of the costal space has nine long, oblique crossveins; in the pterostigmal area, close to the wing apex, SC is connected with C by two short crossveins. R is almost straight, curved slightly apically; RS has broad