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Fossil Insects of the Middle and Upper Permian of European Russia

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Abstract—Fossil insects of European Russia from the Urzhumian to Vyatkian stages are reviewed, new taxa are described, and dynamics of insect taxonomic diversity around the Permian–Triassic boundary in light of the Paleozoic–Mesozoic boundary global extinction problem is analyzed. Traces of interactions between arthropods and plants are analyzed. Insect-bearing deposits of the Late Paleozoic found in the northern and eastern areas of the East European Platform are unique on the global scale in their completeness and continuity, allowing us to trace especially comprehensively the biotic processes that occurred around the boundary described as the time of the greatest biotic catastrophe of the Phanerozoic. A total of 28 genera and 111 species are newly described. Within the range from the Urzhumian to the Permo–Triassic boundary, 15 representative successive assemblages, including 112 families, are recognized (seven in the area in question and eight in other regions of Asia, Australia, and Africa). New tools are developed for the analysis of the dynamics of diversity. These tools show an approximately equilibrium (slightly positive) dynamics in the Urzhumian and Severodvinian and a drop in diversity during the Vyatkian Age. It is shown that Permian insect assemblages acquired a substantially post-Paleozoic pattern much earlier than the end of the Paleozoic. The character of changes that took place in the Induan and Olenekian remains uncertain, but a large-scale extinction event did not occur here: most families that have not been recorded at the beginning of the Triassic are recorded again in the Middle and Upper Triassic. Nevertheless, a biotic crisis probably actually took place, but was reduced to reorganization of the biota's structure, which provided enormous growth of biodiversity over subsequent hundreds of millions of years, rather than resulted in catastrophic extinction. This study is intended for entomologists, stratigraphers, and all readers interested in the biotic events that took place around the Permian–Triassic boundary.

Keywords: Insecta, biodiversity crisis, arthropods–plant interaction, new taxa, insect localities, Middle and Upper Permian, European Russia

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3. RESULTS AND DISCUSSION

PREFACE

The present study is devoted to fossil insects of European Russia from the Urzhumian to Vyatkian in the context of the problem of the global Permian–Triassic biotic crisis, described as the greatest global extinction of the Phanerozoic. The subject of this study was chosen taking into account the fact that continental deposits of the terminal Permian form in the northern and eastern East European Platform a unique almost uninterrupted sequence and contain rather rich fossil insect assemblages and insects, enormously diverse as they are, are a promising object for studying the dynamics of biological diversity (Dmitriev and Zherikhin, 1988; Rasnitsyn, 1988, 1989; Labandeira and Sepkoski, 1993; Alekseev et al., 2001; Ross et al., 2000; Dmitriev and Ponomarenko, 2002; Shcherbakov, 2008; etc.).

The material of this study consists of large collections of fossil insects from Middle and Upper Permian localities of Russia, which were collected over the last decade by expeditions of the Arthropoda Laboratory of the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). To date, the numerous and diverse insects of this time and region have clearly insufficiently been studied. Members of the orders Caloneurida, Hypoperlida, Mischopterida, Paleomanteida, Coleoptera, Jurinida, Panorpida, Trichoptera, Grylloblattida, Perlida, Titanoptera, Orthoptera, and Phasmatoptera are described below. Numerous Hemiptera and Blattida have been identified to family, but, unfortunately, remain undescribed. A total of 27 new genera and 117 new species are described here. Northern, central, and eastern European Russia are of great importance because of the stratigraphic continuity of their Permian–Triassic insect-bearing deposits. The Lower Vyatkian remains to date the only time not characterized with insects from the Urzhumian to Olenekian range. For comparison, in the Permian–Triassic sequence of the Kuznetsk Basin, the second most complete after that of European Russia, Vyatkian (with the exception of the transitional Permian–Triassic, see Chapter 3.1) and Olenekian insect faunas remain unknown.

A review of faunas and descriptions of new taxa are followed by a general conclusion in context of the global dynamics of insect families from the Urzhumian to Olenekian based on available data on local assemblages of this period from Eurasia, Africa, and Australia. The question is discussed of the character of changes in the composition of the largest group of living organisms that took place at the most dramatic boundary in the Phanerozoic history of life, that between the Permian and Triassic, and around this boundary. Approximately balanced (slightly positive) dynamics of diversity has been found in the Urzhumian and Severodvinian, and a drop in biodiversity has been recorded during the Vyatkian. As a result, Permian insect assemblages had acquired a strongly post-Paleozoic pattern markedly earlier than the end of the Paleozoic. The character of changes that occurred during the Induan and Olenekian remain insufficiently understood, although it is evident that a catastrophic extinction of insects was not observed at the end of the Permian, and many families not found in the Early Triassic are mostly recorded again in the Middle to Late Triassic.

Traces giving evidence of interactions between arthropods and plants in the Upper Permian of European Russia are analyzed; some traces are described as new.

The authors of sections in this monograph are listed in the Contents and at the beginning of each section. It should be noted that it was D.A. Rasnitsyn who developed the computer program for optimizing the chronological sequence of fossil assemblages. The results obtained with this program are used in Chapter 3.1. It is planned to provide a description of this program in a separate publication.

D.S. Aristov, January 20, 2012

1. INTRODUCTION. LOCALITIES OF MIDDLE PERMIAN TO LOWER TRIASSIC INSECTS IN EUROPEAN RUSSIA

1.1. Urzhumian and Severodvinian Localities

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In the following chapters, fossil insect localities of European Russia are characterized: five Urzhumian, seven Severodvinian, four Vyatkian, four transitional Permian–Triassic, and one Olenekian. Most of the identifications of insects are based on the materials collected during the last decade by the Arthropoda Laboratory of the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN) and stored in this institution. The material was identified by the following specialists: A.G. Ponomarenko (Coleoptera and Neuroptera), D.E. Shcherbakov (Hemiptera), N.D. Sinitshenkova (Ephemerida, Palaeodictyoptera, and Perlida), D.V. Vassilenko (Odonata), A.S. Bashkuev (Panorpida), A.V. Gorochov (orthopteroids), and P. Vršanský (Blattida). The concept of Blattida used here is based on the phylogenetic system proposed by Vršanský (2000, 2002a, 2002b, 2010a, 2010b) and Vršanský et al. (2002) (Paleozoic groups) and identifications by Vršanský (pers. comm.). Except for the new indigenous taxa, the families are treated as follows. "Argentinoblattidae" follow the concept of *Irreblatta* (Vršanský, 2008a), the last appearances of which come from the Upper Jurassic. The Phyloblattidae (sensu Schneider, 1983) include transitional form to "Argentinoblattidae" (Vršanský, 2010b), common in the Permian and Triassic (Vršanský, 2003a), with a species persisting in the Barremian of Bon Tsagaan (Vršanský, 2003b, 2008b). The concept of the Caloblattinidae follows Vršanský and Ansorge (2007) and excludes the taxa now referred to the Mesoblattinidae sensu stricto The latest record of Caloblattinidae is from the Archingeay amber (Vršanský, 2009).

Deformations possibly representing hereditary mutations (changing the wing geometry) (Vršanský, 2005) are extremely rare in Upper Permian localities, represented by a single deformity among many dozen studied complete wings, suggesting that the lineages were then near their phylogenetic bases.

Urzhumian fossil insects are known in European Russia mostly from the Kargala locality in the Orenburg Region and two geographically close and probably contemporaneous Chepanikha and Kostovaty localities in Udmurtia.

Chepanikha. Udmurtia, Zav'yalovskii District, forest gully in the Rossokha River valley 1.8 km north of the village of Chepanikha (GPS: 56°40.71′ N, 53°38.68′ E). The deposits are traditionally assigned to the Urzhumian Stage (Shcherbakov, 2008; chapter 2.3), although there are serious arguments in favor of considering them Late Kazanian (A.V. Gomankov, pers. comm.). Fossils found in siltstones included plant remains, insects, ostracodes, conchostracans, notostracans, and scales and coprolites of fish. For a more detailed discussion of the Chepanikha locality, see Aristov and Bashkuev (2008).

The insect collection of PIN contains over 300 specimens (collected by the Arthropoda Laboratory, PIN in 2005 and 2006). The prevailing orders are Grylloblattida (22% of all insects), Perlida (14%), Panorpida (10%), and Hemiptera (8%); other orders represented by rather few specimens include Blattida, Coleoptera, Neuroptera, Orthoptera, Paleomateida, Trichoptera, Ephemerida, Odonata, Hypoperlida, and Jurinida.

Hypoperlida Martynov, 1928
- Ischnoneuridae Handlirsch, 1906
    - *?Jarmilacladus patiens* Rasnitsyn et Aristov, sp. nov.

Palaeomanteida Handlirsch, 1906
- Palaeomanteidae Handlirsch, 1906
    - *?Miomatoneurella rossoshana* Rasnitsyn et Aristov, sp. nov.
- Permosialidae Martynov, 1928
    - *Epimastax tshepanikha* Rasnitsyn et Aristov, sp. nov.
    - *Permosialis zavialovensis* Rasnitsyn et Aristov, sp. nov.
    - *Onthomastax coprinus* Rasnitsyn et Aristov, gen. et sp. nov.

Hemiptera Linné, 1758
- Ingruidae Becker-Migdisova, 1960
- Scytinopteridae Handlirsch, 1906
- Pereboriidae M. Zalessky, 1930
- Surijokocixiidae Shcherbakov, 2000
- Serpentivenidae Shcherbakov, 1984
- Prosbolidae Handlirsch, 1906
- Dysmorphoptilidae Handlirsch, 1906 (D.E. Shcherbakov, pers. comm., 2011)

Jurinida M. Zalessky, 1928
- Jurinidae M. Zalessky, 1929
    - *Jurina biarmica* Rasnitsyn et Aristov, sp. nov.

Coleoptera Linné, 1758
- Permocupedidae Martynov, 1933
    - *Permocupes latus* Ponomarenko, sp. nov.
    - *Protocupoides elongatus* Ponomarenko, sp. nov.
- Rhombocoleidae Rohdendorf, 1961
    - *Rossocoleus angustus* Ponomarenko, sp. nov.
    - *R. novojilovi* Ponomarenko, sp. nov.
- Schizophoridae Ponomarenko, 1968
    - Schizophoridae incertae sedis

Panorpida Latreille, 1802
- Permochoristidae Tillyard, 1917
    - *Xenochorista borealis* Novokshonov, 1997
    - *Asiachorista europaea* Bashkuev, 2008
    - *Petromantis udmurtica* Bashkuev, 2008
    - *P. rossica* Handlirsch, 1904
    - *Mesochorista* Tillyard, 1916
- Kaltanidae O. Martynova, 1958
    - *Pseudochorista occidentalis* Bashkuev, 2008
    - *Kamochorista novokshonovi* Bashkuev, 2008 (Novokshonov, 1997; Aristov and Bashkuev, 2008; Bashkuev, 2008)

Trichoptera Kirby, 1815
- Microptysmatidae O. Martynova, 1958
    - *Kamopanorpa maculata* Sukatsheva et Aristov, sp. nov. (known also from the Kostovaty locality; see below)
    - *K. tshepanikhensis* Sukatsheva et Aristov, sp. nov.

Blattida Latreille, 1810
- Mylacridae Scudder 1886
- Phylloblattidae Schneider, 1983 (P. Vršanský, pers. comm., 2011)

Grylloblattida Walker, 1914
- Chauliodititidae Handlirsch, 1906
    - *Miralioma urzhumica* Aristov, 2008
- Liomopteridae Sellards, 1909
    - *Rigidilioma radialis* Aristov, 2004
    - *Parapermula tatarica* Aristov, 2004
    - *Liomopterites novissimus* Aristov, 2004 (Aristov, 2004e; 2008)
- Megakhosaridae Sharov, 1961
    - *Megakhosarina chepanikhensis* Aristov, 2008

Tshekardominidae Novokshonov et Aristov, 2001
Sigmophlebia udmurtica Aristov, 2008
Permulidae Aristov et Storozhenko, 2011
Tshepanichoptera lacera Aristov, 2008 (Aristov, 2008c; Aristov and Storozhenko, 2011)

Perlida Latreille, 1810
Palaeonemouridae Sharov, 1961
Palaeonemoura proximalis Sinitshenkova, 2004 (Sinitshenkova, 2004)
P. repleta Sinitshenkova, sp. nov.
Palaeonemourisca strigosa Sinitshenkova, sp. nov.

Orthoptera Olivier, 1789
Permelcanidae Sharov, 1961
Meselcaninae Gorochov, 1989
Meselcana udmurtica Gorochov, sp. nov.
Oedischiidae Handlirsch, 1906
Tcholmanvissiinae incertae sedis

Kostovaty (=Galevo). Udmurtia, Votkinskii District, right bank of Votkinsk Reservoir (Kama River) 6.4 km downstream from Galevo dock (GPS: 56°54.34′ N, 54°05.29′ E). The deposits are assigned to the Urzhumian Stage (Shcherbakov, 2008; chapter 2.3). Fossils found in siltstones included plant remains, insects, ostracodes, conchostracans, and fish scales.

The number of insect fossils is about 100 specimens (collected by the Arthropoda Laboratory, PIN, 2006). The insects are represented by 11 orders: Ephemerida, Hemiptera, Palaeomanteida, Coleoptera, Neuroptera, Panorpida, Trichoptera, Blattida, Grylloblattida, Perlida, and Orthoptera. The prevalent insect fossils are nymphs of stoneflies and mayflies (about half of the specimens); other, less abundant taxa are grylloblattids (17%) and homopterans (11%); other orders are rather infrequent (Shcherbakov, 2008).

Palaeomanteida Handlirsch, 1906
Permosialidae Martynov, 1928
Permosialis sp.

Coleoptera Linné, 1758
Asiocoleidae Rohdendorf, 1961
Schizotaldycupes pubescens Ponomarenko, sp. nov.
Rhombocoleidae Rohdendorf, 1961
Rhombocoleites uralensis Ponomarenko, sp. nov.

Panorpida Latreille, 1802
Permochoristidae Tillyard, 1917
Asiachorista O. Martynova, 1958 (A.S. Bashkuev, pers. comm., 2011)

Trichoptera Kirby, 1815
Microptysmatidae O. Martynova, 1958
Kamopanorpa grossa Novokshonov, 1993
K. maculata Sukacheva et Aristov, sp. nov.

Gryloblattida Walker, 1914
Liomopteridae Sellards, 1909
Paraliomopterum rectum Aristov, 2004 (Aristov, 2004e)
Lemmatophoridae Sellards, 1909
Kostovatoprisca acuminata Aristov, 2008 (Aristov, 2008c)

Kargala. Orenburg Region, Sakmarskii District, dumps (Dmitrievskie, Kontorskie, Kuz'minskie, Levskie, Nikolaevskie, Nikol'skie, Semenovskie, and Ural'skie) of the Kargala copper mines. Urzhumian Stage, Amanak Formation, *Estemmenosuchus uralensis* and *Ulemosaurus svijagensis* zones (Shcherbakov, 2008; chapter 2.3). Fossils found in siltstones of lake origin include plant remains, insects, fish, and tetrapods.

The collection of insects from this locality, stored in PIN (materials collected by I.A. Efremov and M.N. Chueva in 1929, E.V. Permyakova in 1931, and O.M. Martynova in 1938), includes over 300 specimens. A small amount of material is stored in the Karpinsky All-Russia Geological Research Institute (VSEGEI, St. Petersburg) and in Kazan Federal University (Kazan). Insects are represented by 12 orders: Ephemerida, Odonata, Caloneurida, Hemiptera, Coleoptera, Corydalida, Neuroptera, Panorpida, Blattida, Grylloblattida, Perlida, and Orthoptera. The dominant orders are Blattida and Grylloblattida, which make up a half and a third of all insect fossils, respectively; other orders are infrequent (Shcherbakov, 2008). A distinctive feature of Kargala is the fact that the diversity and abundance of Hemiptera here are extremely low for the Permian (less than ten specimens).

Ephemerida Latreille, 1810
Ephemerida incertae sedis
Phtartus rossicus Handlirsch, 1904
P. necajevi Handlirsch, 1904 (Handlirsch, 1904; Chernova, 1962)

Odonata Fabricius, 1792
Permolestidae Martynov 1932
Scytolestes stigmalis Martynov, 1937
Epilestes kargalensis Martynov, 1937 (Martynov, 1937)
Meganeuridae Handlirsch, 1906
Megatypus kargalensis Martynov, 1932 (Martynov, 1932)

Caloneurida Handlirsch, 1906
Caloneuridae Handlirsch, 1906
Eohymen maculipennis Martynov, 1937 (Martynov, 1937)

Hemiptera Linné, 1758
Surijokocixiidae Shcherbakov, 2000
Scytocixius mendax Martynov, 1937
Pereboridae M. Zalessky, 1930
Scytophara extensa Martynov, 1937 (Martynov, 1937)

Coleoptera Linné, 1758
Rhombocoleidae Rohdendorf, 1961
Curculiopsis ellipticus Martynov, 1937 (Martynov, 1937)
Rhombocoleites adumbratus Ponomarenko, 1969 (Ponomarenko, 1969)

Permocupedidae Martynov, 1933

Kaltanicupes kargalensis Ponomarenko, 1963 (Ponomarenko, 1963)

Taldycupedidae Rohdendorf, 1961

Tecticupes martynovi Ponomarenko, sp. nov.

Corydalida Leach, 1815

Corydalida indet. (the order is represented by a single unnamed larva described as *Permosialis* sp.; Sharov, 1953, see photograph in: Rasnitsyn and Quicke, 2002, text-fig. 246).

Neuroptera Linné, 1758

Permithonidae Tillyard 1922

Sialidopsis kargalensis M. Zalessky, 1926 (Zalessky, 1926)

S. similis Martynov, 1937 (Martynov, 1937)

Neuroptera incertae sedis

Parasisyra kargalica G. Zalessky, 1933 (Zalessky, 1933; Novokshonov, 1996)

Panorpida Latreille, 1802

Permochoristidae Tillyard, 1917

Petromantis stigma O. Martynova, 1942

P. mirabilis (O. Martynova, 1942)

Panorpida incertae sedis (Novokshonov, 1997)

"Permochorista" kargalensis O. Martynova, 1942 (Martynova, 1942)

"P." ingloria O. Martynova, 1942 (Martynova, 1942)

"P." minuta (G. Zalessky, 1933) (Zalessky, 1933)

Blattida Latreille, 1810

Phyloblattidae Schneider, 1983

Aissoblatta rossica Handlirsch, 1904

A. orenburgensis Handlirsch, 1904 (Handlirsch, 1904)

A. parvula Martynov, 1937

Phyloblatta uralensis Martynov, 1937 (Martynov, 1937)

Spiloblattinidae Handlirsch, 1906

Kargaliinae Vishniakova, 1993

Kargalia orenburgensis Vishniakova, 1993

K. pectinacea Vishniakova, 1993 (Vishniakova, 1993)

Blattida incertae sedis

Amekeoblatta elegans G. Zalessky, 1933 (Zalessky, 1933)

The record of Poroblattinidae in Kargala (Zalessky, 1933), based on *A. elegans*, is erroneous: in the opinion of P. Vršanský, this genus does not belong to poroblattinids. For determining the family to which this species belongs, re-examination of the holotype is required (P. Vršanský, pers. comm., 2011).

Grylloblattida Walker, 1914

Liomopteridae Sellards, 1909

Khosara permiakovae Martynov, 1937 (Martynov, 1937)

Kargalella subcostalis Martynov, 1937

K. gibbosa Aristov, 2004 (Martynov, 1937; Aristov, 2004c; Aristov et al., 2009a)

Liomopterites amanakicis Aristov, 2009

Expartolioma urzhumica Aristov, 2009 (Aristov, 2009d)

Megakhosaridae Sharov, 1961

Megakhosara fasciipennis Martynov, 1937 (Martynov, 1937; Aristov, 2004b)

M. nana Aristov, 2009 (Aristov, 2009d)

Syndesmorpha composita Martynov, 1937 (Martynov, 1937; Aristov, 2004b)

Kargalokhosara terraiffosa Aristov, 2008 (Aristov, 2008b)

Ideliidae M. Zalessky, 1929

Metidelia kargalensis Martynov, 1937 (Martynov, 1937)

Skalicidae Kukalová, 1964

Urzhumskalicia kargalensis Aristov, 2009

Kargalopteridae Aristov, 2009

Kargaloptera connexa Aristov, 2009

Urzhumia sakmarica (Aristov, 2009) (*Urzhumia* Aristov, nom. nov. = *Kargalia* Aristov, 2009, non Vishniakova, 1993) (Aristov, 2009d)

Perlida Latreille, 1810

Palaeonemouridae Sharov, 1961

Kargaloperla exuperata Sinitshenkova, 1987 (Sinitshenkova, 1987)

Palaeoperlidae Sharov, 1961

Permoleuctropsis gracilis Martynov, 1937 (Martynov, 1937)

Orthoptera Olivier, 1789

Pruvostitidae M. Zalessky, 1929

Kargalariinae Sharov, 1968

Kargalaria maculata Sharov, 1968 (Sharov, 1968; Gorochov, 1995)

Insecta incertae ordinis

Homoeodictyidae Martynov, 1937

This family was described in the order Prothorthoptera (Martynov, 1937); currently, it appears impossible to determine to which order it belongs (Rasnitsyn, 2002).

Homoeodictyon elongatum Martynov, 1937

Insecta incertae sedis

Dyadozoarium pachypus Handlirsch, 1904

This genus was assigned to Paraplecoptera (=Grylloblattida) incertae sedis (Handlirsch, 1904; Sharov, 1962); judging from the figure, the insect was a specialized phytophile and had large legs with tibia directed forward in all three pairs; this mode of life and morphology of the legs are atypical of Grylloblattida. This fact and the fact that the pattern of its venation could not be interpreted prevents the assignment of this insect to a certain order.

Chalcorychus walchiae Handlirsch, 1909

This species was originally described in Perlida (Handlirsch, 1909) and then transferred to Prothorthoptera (Martynov, 1937); the published figure of the distal halves of its wings prevents the assignment of this insect to a certain insect order; it can only be assumed that it does not belong to stoneflies, because the branches of its R are too dense.

Severodvinian fossil insects of European Russia are known mostly from the Novo-Aleksandrovka, Babintsevo, and Kul'chumovo localities in the Orenburg Region and Isady in the Vologda Region.

Deposits of the lower layers of the Lower Severodvinian Substage (Sukhona Formation, Verkhnyaya Toz'ma Member; *Tatarskie otlozheniya...,* 2001; *Postanovleniya...,* 2006) include those of the **Kopylovo** locality (Vologda Region, Nyuksenskii District, left bank of the Sukhona River 1.2 km downstream from the eastern limits of the village of Kopylovo and 1.3 km upstream from the mouth of the Yurmen'ga River; GPS: 60°35′25.19″ N, 45°06′56.23″ E). In 2011, the pronotum of a Grylloblattida was found in these localities by an expedition of the Arthropoda Laboratory, PIN.

Kul'chumovo. Orenburg Region, Saraktashskii District, gully on the right bank of the Sakmara River 3 km downstream from the village of Kul'chumovo (GPS: 51°52′52.76″ N, 56°14′48.30″ E). The deposits are considered to belong to the lower layers of the Upper Severodvinian Substage, Vyazovka Formation (V.K. Golubev, pers. comm., 2011); they represent siltstones of lake origin containing plant remains, conchostracans, ostracodes, insects, the amphibian Chroniosuchidae gen. indet., and the gliding reptile *Rautiania* (family Weigeltisauridae).

A total of about 50 insect fossils have been collected by PIN expeditions in 2005 and 2007. The insect collection stored in PIN contains Hemiptera, Coleoptera, Jurinida, Panorpida, Blattida, and Grylloblattida. The dominant order is Blattida; among the other orders, Coleoptera is relatively abundant.

Coleoptera Linné, 1758
- Rhombocoleidae Rohdendorf, 1961
  - *Aenigmocoleus uralensis* Ponomarenko, sp. nov.
  - *Rossocoleus sakmara* Ponomarenko, sp. nov.
- Schizocoleidae Rohdendorf, 1961
  - *Schizocoleus major* Ponomarenko, sp. nov.
- Permosynidae Tillyard, 1924
  - *Sakmaracoleus orenburgensis* Ponomarenko, gen. et sp. nov.
  - *Permosyne angustior* Ponomarenko, sp. nov.

Jurinida M. Zalessky, 1928
- Jurinidae M. Zalessky, 1929
  - *?Eoglosselytrum kultshumovense* Rasnitsyn et Aristov, sp. nov.

Panorpida Latreille, 1802
- Permochoristidae Tillyard, 1917
  - Agetopanorpinae Carpenter, 1930 (A.S. Bashkuev, pers. comm., 2011)

Blattida Latreille, 1810
- Caloblattinidae Vršansḱ et Ansorge, 2000
- Phyloblattidae Schneider, 1983 (P. Vršansḱ, pers. comm., 2011)

The same deposits are probably represented by the **Sakmara, Cherepanovka**, and **Staroseika** localities in the Saraktashskii District, Orenburg Region. In Sakmara (upper reaches of a gully, right tributary of the Sakmara River, downstream of the village of Kul'chumovo), V.A. Goryainov found in 1961 a single cockroach, *Aissoblatta* sp. (Phylloblattidae). V.P. Tverdokhlebov found in 1963 and 1964 single impressions of Phylloblattidae (left bank of the Buruncha River near the village of Cherepanovka) and "Argentinoblattidae" in a borehole near the village of Staroseika (borehole 41; depth of 20.5 m). The materials are stored in PIN.

Upper Severodvinian insects have been found in the localities of Babintsevo (Orenburg Region), Opoki, and Isady (both Vologda Region).

Babintsevo. Orenburg Region, Grachevskii District, right slope of the gully, right tributary of the Konduzla River 2.8 km northeast of the village of Babintsevo (GPS: 53°13′2.60″ N, 52°50′20.15″ E). Upper Severodvinian Substage, *Chroniosaurus dongusensis* Subzone of the *Proelginia permiana* Zone (Ivakhnenko et al., 1997; *Postanovleniya ...,* 2006). The material is from sandstones of the former riverbed origin, containing plant remains, conchostracans, and insects.

The insects were collected by a joint expedition of the Arthropoda and Lower Tetrapod laboratories, PIN, in 2007. A total of about 40 insect fossils have been found, including members of the orders Odonata, Coleoptera, Panorpida, and Blattida (the collection is stored in PIN). Blattida make up the overwhelming majority of specimens; members of other orders are rather infrequent.

Odonata Fabricius, 1792
- ?Permaeschidae Martynov 1931 (D.V. Vassilenko, pers. comm., 2011)

Coleoptera Linné, 1758
- Schizocoleidae Rohdendorf, 1961
  - *Uskatocoleus uralensis* Ponomarenko, sp. nov.

Panorpida Latreille, 1802
- Permochoristidae Tillyard, 1917
  - *Mesochorista* Tillyard, 1916 (A.S. Bashkuev, pers. comm., 2011)

Blattida Latreille, 1810
- Phyloblattidae Schneider, 1983
  - *Aissoblatta* Handlirsch, 1904
- Mylacridae Scudder 1886 or Necymylacridae Durden, 1969 (P. Vršanský, pers. comm., 2011).

Deposits of the middle layers of the Upper Severodvinian Substage (Isady Member of the Poldarsa Formation; *Tatarskie otlozheniya ...,* 2001; *Postanovleniya...,* 2006) are represented also in the **Opoki** locality. This locality is situated on the left bank of the Sukhona River opposite the former village of Opoki, upstream from the mouth of Svyatoi Creek, in the Velikoustyugskii District of the Vologda Region (GPS: 60°35′40.61″ N, 45°29′37.89″ E). In 2011, an elytron of a Psylomorpha hemipteran was found in this locality by an expedition of the Arthropoda Laboratory, PIN.

Isady, the largest known Upper Permian fossil insect locality in the world (lower part of the Kalikino Member of the Poldarsa Formation, uppermost Severodvinian Stage) in the Vologda Region, is treated separately due to its uniqueness (Chapter 1.2).

The age of the localities of Novo-Aleksandrovka (Orenburg Region), Tuembetovo and Yamansarovo (both Bashkiria), and Beloshchel'e (Arkhangelsk Region) has not been determined more precisely than the Severodvinian.

Novo-Aleksandrovka. Orenburg Region, Tul'ganskii District, left bank of the Kuplya River 6 km from the village of Troitskoe. Severodvinian Stage (Shcherbakov, 2008), Vyazovka Formation. The deposits probably belong to the middle of the Severodvinian Stage (Gomankov and Meyen, 1986). The material was found in lake siltstones containing plant remains, ostracodes, conchostracans, insects, and fish scales.

Insects from this locality were collected by S.V. Meyen (in 1975), A.V. Gomankov (in 2004), and expeditions of the Arthropoda Laboratory, PIN (in 2002 and 2004). A total of over 300 insect specimens have been collected, including members of 12 orders: Odonata, Hemiptera, Palaeomanteida, Coleoptera, Jurinida, Neuroptera, Panorpida, Blattida, Grylloblattida, Perlida, Orthoptera, and Mesotitanida. The dominant order is Blattida, followed by the less abundant Hemiptera and Perlida (Shcherbakov, 2008).

Odonata Fabricius, 1792
  Meganeuridae Handlirsch, 1906
Hemiptera Linné, 1758
  Prosbolopseidae Becker-Migdisova 1946
  Prosbolidae Handlirsch, 1906
  Ingruidae Becker-Migdisova, 1960
  Scytinopteridae Handlirsch, 1906
  Stenoviciidae Evans, 1956
  Pereboriidae M. Zalessky, 1930
  Surijokocixiidae Shcherbakov, 2000
  Dysmorphoptilidae Handlirsch, 1906
  Protopsyllidiidae Carpenter, 1931
  (D.E. Shcherbakov, pers. comm., 2011)
  Coleoptera Linné, 1758
  Permocupedidae Martynov, 1933
    Tatarocupes granulatus Ponomarenko, 2004
  Rhombocoleidae Rohdendorf, 1961
    Karakanocoleus europeus Ponomarenko, 2004
    Erunakicupes brevis Ponomarenko, 2004
    Rhombocoleus gomankovi Ponomarenko, sp. nov.
  Schizocoleidae Rohdendorf, 1961
    Schizocoleus longus Ponomarenko, 2004
    S. glabrus Ponomarenko, 2004
    S. minimus Ponomarenko, sp. nov.
    Pseudochrysomelites ovum (Ponomarenko, 2004)
    P. robustus (Ponomarenko, 2004)
    (Ponomarenko, 2004)
  Asiocoleidae Rohdendorf, 1961
    Tetrocoleus orenburgensis Ponomarenko, sp. nov.
    Bicoleus cuplensis Ponomarenko, gen. et sp. nov.
Panorpida Latreille, 1802
  Permochoristidae Tillyard, 1917
    Mesochorista Tillyard, 1916
    Asiachorista O. Martynova, 1958
    (A.S. Bashkuev, pers. comm., 2011)
Blattida Latreille, 1810
  Phyloblattidae Schneider, 1983
  Subioblattidae Schneider, 1983
  "Argentinoblattidae" Martins-Neto et Gallego, 2005
    Voltziablatta Papier et Grauvogel-Stamm, 1995
    (P. Vršanský, pers. comm., 2011)
Grylloblattida Walker, 1914
  Chauliodititae Handlirsch, 1906
    Chauliodites gomankovi Aristov, 2008
    (Aristov, 2008a)
  Geinitziidae Handlirsch, 1906
    Shurabia Martynov, 1937 (Aristov, 2004b)
  Liomopteridae Sellards, 1909
    Alekhosara reticulata Aristov, 2008

The genus was erroneously described in the family Megakhosaridae (Aristov, 2008b); the absence of posterior branches of CuA, unknown in other magakhsarids, and the broad costal space suggests that this genus should be transferred to the family Liomopteridae.

  Tshekardominidae Novokshonov et Aristov, 2002
  Kuplya minutissima Aristov, 2013 (Aristov, 2013a)
Perlida Latreille, 1810
  Palaeoperlidae Sharov, 1961
    Palaeoperla perfracta Sinitshenkova, 1987
    (Sinitshenkova, 1987)
  Palaeonemouridae Sharov, 1961
    Palaeotaeniopteryx perlonga Sinitshenkova, 2004
    P. distalis Sinitshenkova, 2004
    Palaeonemoura lepida Sinitshenkova, 2004
    P. petaloidea Sinitshenkova, 2004
    P. duplicata Sinitshenkova, 2004
    P. riparia Sinitshenkova, 2004

P. apicalis Sinitshenkova, 2004
P. remota Sinitshenkova, 2004
Palaeonemourisca subita Sinitshenkova, 2004 (Sinitshenkova, 2004)

Orthoptera Olivier, 1789
Permelcanidae Sharov, 1962
Meselcaninae Gorochov, 1989
Meselcana ?vologodica Gorochov, sp. nov.

?Mesotitanida Tillyard, 1925
Deinotitanidae Gorochov, 2007, stat. nov.
Deinotitan orenburgensis Gorochov, 2007 (Gorochov, 2007b)

The localities of **Tuembetovo** (Bashkiria, Kurgachinskii District, left bank of the Tashli River, 350 m east and 1.2 km east-northeast of the village of Tuembetovo) and **Yamansarovo** (Bashkiria, Kuyurgazinskii District, right bank of a creek in the central part of the village of Yamansarovo), which are geographically close to Novo-Aleksandrovka, are probably also Severodvinian. In 1964, E.V. Klimov found in these localities several cockroaches of the family Phylloblattidae, which are stored in PIN.

The **Beloshchel'e** locality is assigned to the Severodvinian (Beloshchel'e Formation). It is situated on the right bank of the Mezen River, Leshukonskii District, Arkhangelsk Region. The insects found in this locality are represented by one specimen of the scorpionfly *Mezena alba* Novokshonov, 1995 (Permochoristidae), collected by V.A. Malina in 1962 (Novokshonov, 1995).

1.2. Severodvinian Isady (=Mutovino) Locality in the Vologda Region

1.2.1. History of Studies

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Recently, as a result of expeditions organized mostly by the Arthropoda Laboratory of PIN, a gray lens opposite the village of Isady, Vologda Region, turned into the largest known locality of Upper Permian insects. During the last five years (2007 to 2012), paleoentomological excavations have annually been performed in this outcrop and are likely to be continued in the future. Edemskii (1928) was the first to mention the Isady lens, while the first specimens were collected there in the time of V.P. Amalitzky, probably, in the late 19th century. During the latter half of the 20th century, the Sukhona section was studied by dozens of expedition teams from various scientific and geological prospecting institutions of Russia and even by foreign scientists. Since information on all these investigators cannot be included in this review, only the principal work done in this area is discussed below. The information provided by M.G. Minikh, A.V. Gomankov, M.P. Arefiev, and V.K. Golubev was very helpful for the preparation of this review, and the author is grateful to them all.

The study of the Upper Permian deposits of the Sukhona River started as early as the first half of the 19th century. In 1840–1841, expeditions of R.I. Murchison and J.H. Blasius worked at these sections (Murchison et al., 1845; Barbot de Marny, 1868). The discoverers of the Permian System failed to find any traces of fossil flora or fauna in these outcrops. This probably resulted in the idea generally accepted in the scientific community for a long time that these deposits were "mute." Nevertheless, studies of deposits on the banks of the Sukhona River continued. In 1843, count Alexander von Keyserling carried out a large-scale expedition over the northern rivers of Russia. In the environs of the village of Monastyrikha (80 km downstream from Tot'ma on the Sukhona River), he found two brachiopod impressions, which he identified as *Terebratula elongata* and *T. geinitziana* (Keyserling, 1846). The origin of these specimens from parental Permian deposits was subsequently questioned. The brachiopods probably come from rocks transported by a glacier, as supposed by the outstanding Russian geologist N.P. Barbot de Marny. In 1864, he organized an expedition to northern European Russia, the tasks of which included a geological survey of the Sukhona River. In his publication (Barbot de Marny, 1868), he reported numerous findings of brachiopods, bryozoans, and mollusks at the upper reaches of the river, especially in the core samples provided by salt manufacturers in the Tot'ma area. However, as for the lower reaches of the Sukhona River, Barbot de Marny restricted himself to the statement of the generally accepted belief: "The local formations are in the full sense *terrains muets* [French for 'mute lands']."

The myth about the hopelessness of paleontological studies in the Northern Dvina River was finally destroyed in the late 19th century. This breakthrough is associated with the name of the great Russian scientist Vladimir Prokhorovich Amalitzky (1860–1917). In the course of his long-term work at the Sukhona and Northern Dvina rivers, he discovered a rich fauna of aquatic and terrestrial amphibians and reptiles represented by the labyrinthodont *Dvinosaurus*, parareptile *Scutosaurus*, therapsids *Inostrancevia* and *Dvinia*, and others. These findings caused a true sensation in the scientific community and subsequently formed the core of the Severodvinian gallery in the Paleontological Museum in Moscow, providing the foundation for the establishment of the museum itself. Most of the specimens were collected by Amalitzky at the Lesser Northern Dvina River, in a large sandy lens of the Sokolki locality near the town of Kotlas in 1899–1914. However, in 1897, in the course of prospecting work, Amalitzky carried out an expedition along the Sukhona River. In his report on this expedition, Amalitzky (1897) mentioned the finding of a fish skeleton of the family Palaeoniscidae and many ganoid scales in the area of the Gorodok locality. These specimens were probably collected in the Isady lens (V.K. Golubev, pers. comm., 2012). Unfortunately, as Amalitzky discovered the Sokolki locality at the lower reaches of the Lesser Northern Dvina River, subsequent work was focused for many years on this locality and the study of outcrops on the banks of the Sukhona River was virtually stopped.

It was restarted in the 1920s. By that time, the bone-bearing beds of Sokolki were completely exhausted and further excavation required great efforts unrealizable for the Academy of Sciences. The Northern Dvina Commission headed by the Academician A.P. Karpinsky was established and organized prospecting exploration of outcrops on the river banks of the Northern Dvina River basin with the purpose of finding new localities similar to Sokolki. In 1925–1926, M.B. Edemskii, a geologist, ethnographer, and local history scholar, performed, as part of this project, a large-scale reconnaissance at the Sukhona, Yug, and Lesser Northern Dvina rivers. In his report (Edemskii, 1928), the description of the “Mutovino lens” is given. According to the description, the lens is located immediately at the mouth of the Mutovka River and probably has nothing in common with the locality discussed here. However, in the same study, a description of an unnamed gray lens 1 km downstream from Mutovino, with abundant outcrops of carbonaceous matter is provided. This is apparently the first description of the Isady locality. Edemskii pointed out that stems of carbonized wood up to half a meter long and fragments of bones and scales were found in this lens.

In the 1930s–1960s, small-scale geological mapping and detailed stratigraphic studies of the Upper Permian sections of the Sukhona River were performed. This period is marked by work of E.M. Lyutkevich, who recognized the Nizhnyaya Ust’ya, Sukhona, and Severnaya Dvina formations in the Tatarian deposits (Lyutkevich, 1955). This stratigraphic results were subsequently officially approved, creating the foundation for further studies. The fundamentals of a detailed stratigraphic division of the deposits excavated at the Sukhona River were outlined in the studies of Plotnikov (1948, 1949) and Pakhtusova (1962).

In the 1970s, medium-scale geological mapping of the area in question was performed under the direction of Buslovich (1975). At the same time employees of Saratov State University, the Geological and Paleontological institutes of the Academy of Sciences of the Soviet Union (later, Russian Academy of Sciences), and a number of other institutions started working at the Sukhona sections. Expeditions of Saratov geologists (A.V. Minikh, M.G. Minikh, I.I. Molostovskaya, G.I. Tverdokhlebova) worked at Sukhona localities in 1971–1973, 1984, and 2001 (M.G. Minikh, pers. comm., 2012). They prepared a detailed geological description of many sections located at the Sukhona River, including the Mutovino lens (*Opornyi razrez ...*, 1981; *Tatarskie otlozheniya...,* 2001). These studies were based mostly on fossil tetrapods, fishes, and shells of bivalves, gastropods, ostracodes, and conchostracans.

The first insect remains in Isady were found by an expedition headed by V.A. Molin (Institute of Geology, Komi Scientific Center, Academy of Sciences of the USSR) in 1975. Three years later, he organized a large expedition to Isady, with the participation of employees of the Institute of Geology and trusts Polyarnouralgeologiya and Tatneftegazrazvedka and paleobotanists of the Geological Institute of the Academy of Sciences of the USSR S.V. Meyen and A.V. Gomankov, who prepared a detailed paleobotanical description of the Sukhona River (Gomankov and Meyen, 1986; A.V. Gomankov, pers. comm., 2012).

In the 1980s and 1990s, various specialized studies were performed at localities of the Sukhona section, including Isady. In 1988, A.V. Gomankov worked there. A research group of the Paleogeography Laboratory of the Earth Crust Institute, St. Petersburg State University, prepared a detailed description of large sandy lenses of the Sukhona and Northern Dvina rivers, including the Isady lens (Verzilin et al., 1993). An expedition group of the Institute of Geography, Russian Academy of Sciences, and Moscow State University (V.O. Targul’yan, E.Yu. Yakimenko, S.A. Inozemtsev, and M.P. Arefiev) performed studies of Permian soils at the Sukhona River in 1997. The paleosols were found above the top of the Isady lens. Isolated plant roots found in Isady were later mentioned by Arefiev and Naugolnykh (1998). In 2009, samples of paleosols were collected in Isady by the Geological and Paleontological Expedition (headed by M.P. Arefiev) of St. Alexius Hermitage.

From the 1990s, Permian deposits of the Sukhona River became a subject to scrupulous studies by workers of the Paleontological Institute of the Russian Academy of Sciences. During the last two decades, more than ten expeditions were carried out, both with the purpose of complex studies of the section and directly for excavations in Isady. Considerable contributions to this work were made by the researchers V.V. Bulanov, V.K. Golubev, Yu.M. Gubin, M.F. Ivakhnenko, and A.A. Kurkin (Paleoherpetological Laboratory) (Ivakhnenko et al., 1997; Golubev, 2000), N.E. Zavialova and E.V. Karasev (Paleobotany Laboratory), and D.S. Aristov, A.S. Bashkuev, O.V. Ryzhkova, D.E. Shcherbakov, and D.V. Vassilenko (Arthropod Laboratory).

In 2005, the first specialized paleontological expedition to Isady was carried out (headed by D.E. Shcherbakov). In 2007 and 2008, insects were collected in Isady by paleoherpetological expeditions (headed by A.A. Kurkin). However, most of the material, over 3000 specimens, were collected during the last three years by expeditions headed by D.S. Kopylov (2009, 2011), E.V. Karasev (2010), and D.E. Shcherbakov (2011). These were the materials that provided the basis for this monograph.

1.2.2. Historical Geology

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The Late Permian Mutovino (=Isady) locality, Vologda Region, and enclosing deposits are described below. The locality has yielded plants, bivalves, insects, ostracodes, conchostracans, fish, and tetrapods. The locality is the uppermost part of the Upper Severodvinian Substage (of the Putyatinian Horizon), near its boundary with the Vyatkian Stage (Bykovian Horizon), in the lower part of the normal polarity magnetozone N_2P. The locality was formed in the marginal part of the delta of a river that originated on the Baltic shield.

The Upper Permian (Tatarian) of the East European Platform is formed mostly by rocks of lacustrine–alluvial origin. The diversity and abundance of fossilized remains of organisms in these deposits is usually so low that, on the face of it, they look absolutely "mute." Co-occurrences of several large taxa in one bed are infrequent here and localities where almost all significant terrestrial and aquatic taxa are present are very few. A locality of this kind is situated on the Sukhona River near the Mutovino site in the Velikoustyugskii District of the Vologda Region (Fig. 1). The riverbed makes a little northward curve here between the villages of Purtovino and Isady. The left, northern bank, washed away during the flood is a 50-m-high and almost 3-km-long steep slope cliff, composed of the banded strata of gray and red Permian rocks. Since erosion is not very intense, the bank is partly covered with areas of dense tree and shrub vegetation; there is no continuous natural exposure of bedrocks (Fig. 2). In the middle part of this outcrop, 2.5 km downstream from the mouth of the Mutovka River, 1.2 km downstream from the Mutovino site, 0.9 km upstream from the village of Isady (Nizhnie Isady pier), and 0.6 km downstream from the village of Purtovino (60°36′56″ N, 45°36′55″ E[1])), there is a large lens of clay and siltstone deposits, containing abundant fossil plant remains, ostracodes, phyllopods, insects, bivalves, fish, and tetrapods. This locality is known in the scientific literature under several different names: Mutovino (as a vertebrate locality : Edemskii, 1928; Efremov and Vjuschkov, 1955; *Opornyi razrez ...,* 1981; Verzilin et al., 1993; Ivakhnenko et al., 1997; Golubev, 2000; *Tatarskie otlozheniya ...,* 2001; Minikh and Minikh, 2009), Isady (as a locality of plants, ostracodes, and insects: *Verkhnepermskie ...,* 1984; Gomankov and Meyen, 1986; *Tatarskie otlozheniya ...,* 2001), and Purtovino (Olfer'ev, 1974; *Opornyi razrez ...,* 1981).

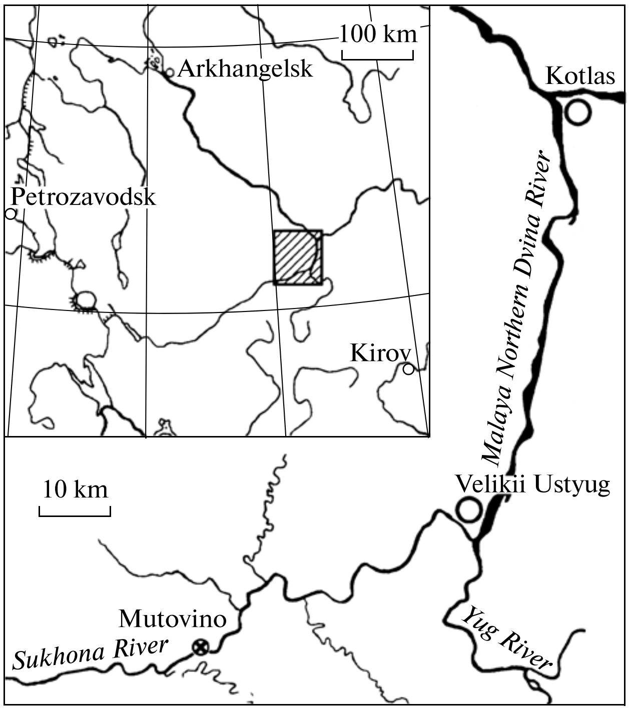

Fig. 1. Geographic position of the Mutovino (=Isady) locality of Late Permian nonmarine organisms, Severodvinian Stage of the Vologda Region.

The Mutovino section was repeatedly studied by different specialists (Verzilin et al., 1993; Edemskii, 1928; Efremov and Vjuschkov, 1955; *Opornyi razrez ...,* 1981; Minikh and Minikh, 1989; *Tatarskie otlozheniya ...,* 2001), including me in 1993, 1997, 2001, and 2012 (Golubev, 2000). In the late 1960s, N.A. Pakhtusova recognized on its basis the Mutovino Beds and the Isady and Purtovino members in the local stratigraphic scale (Golubev, 2000). In 2004, the section was accepted as the limitotype and hypostratotype of the Vyatkian Stage, Tatarian Series, Permian System, by a decision of the Permian System Commission, Interdepartmental Stratigraphic Committee of Russia (Commission for the Permian System ..., 2006). The resolution was approved by the Interdepartmental Stratigraphic Committee in 2005 (Resolution on the Modernization ..., 2006). The section is also suggested as the limitotype of the Bykovian Horizon and, along with other sections located upstream and downstream on the Sukhona River (between the village of Poldarsa and the Salarevo site), as the hypostatotype of the Putyatinian and Bykovian horizons (Golubev et al., 2009).

A lithogenetic, stratigraphic, and paleontological description of this section, which is particularly important for the Permian stratigraphy, is given below.

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[1] Datum: Pulkovo 1942.

Fig. 2. Mutovino outcrop on the left bank of the Sukhona River opposite the village of Purtovino (Vologda Region, Velikoustyugskii District). A large part of the bank slope within this outcrop is covered by dense arboreal vegetation. The lower limit of the forest zone does not descend lower than the red bed outcrop in the upper part of the Purtovino Member, Poldarsa Formation: Beds 27–35 of the section described here (central part of the photograph). In the left part of the photograph, in the middle area of the slope, the Mutovino lens outcrops. Being less durable than the enclosing rocks, they are easily broken, crumbling and slipping down the slope. As a result, the lower part of the lens is only partially covered with herbs, shrubs, and young trees and the base of the bank in this area of the outcrop is covered by scree, strongly overgrown with herbs. Only the axial part of the lens, the area of its maximum thickness is completely exposed (1). The upper part of the lens deposits is strongly watered here. A small stream runs from this area down the slope; the water in this stream is strongly mineralized and hardly suitable for drinking, judging from its smell and taste. A good natural outcrop of the bedrocks is located approximately 300 m downstream the river from the edge of the lens (2). The main portion of the deposits enclosing the lens was described just in this area.

Description of the Section of Enclosing Deposits

The lower part of the section is described at the eastern margin of the Mutovino lens. The following beds have been recognized here (on August 7, 1997), from the shoreline of the river upward in the section (Fig. 3):

Poldarsa Formation

Isady Member

1. Dark brown, pink, massive, strongly calcareous, slaking, silty clay, exposed thickness of 0.75 m.

2. Gray, massive, strongly calcareous clay, 0.6 m thick.

3. Gray, with green interbeds, massive, thick-platy, strong limestone, with small thin root voids, with ostracodes, with interbeds and lenses of clayey limestone, purple silty clay, and gray massive calcareous clay, 2.5 m thick.

Purtovino Member

4–7. Dark gray clay with a cherry tinge, massive, calcareous, with gray worm-shaped streaks (plant roots), with interbeds (up to 0.1 m thick) of gray massive limestone with brown streaks. Fossils found in clays include the ostracodes *Prasuchonella stelmachovi* (Spizh.), *Sinusuella* aff. *ignota, Suchonellina inornata* Spizh., *S. inornata* var. *macra* (Lun.), *S. parallela* Spizh. (*Tatarskie otlozheniya ...,* 2001), 0.8 m thick.

8. Gray, massive, clayey siltstone, 0.5 m thick.

170 m downstream from this point, the following deposits overlie Bed 8:

9–13. Dark brown with green spots, massive, calcareous clay; in the lower part of the bed (0.15 m), with an interbed of gray–green massive clayey limestone with root voids; in the upper part of the bed, with an interbed of massive calcareous clay with fine brown–red intertwining streaks (0.35 m), 1.7 m thick.

14. Reddish brown clay with green polka dots (sporadic regularly circular spots up to 10 mm in diameter, representing gleization areas around organic detritus), massive, nonplastic, silty, 1.55 m thick.

15. Gray–brown siltstone with irregular dull greenish mottles, massive, clayey, 1.45 m thick.

16–20. Alternation of clays: (1) pink, thin-layer, strongly calcareous clay and (2) red–brown clay with sparse green polka dots up to 10 mm in diameter, massive, weakly silty; 1.45 m thick.

21. Gray clay, with a bluish tint in the outcrop, thin-layer horizontally, nonsilty, with shells of the ostracodes *Prasuchonella stelmachovi* (Spizh.), Sinusuella ignota Spizh., *Suchonellina* cf. *parallela,* and *S. futschiki* (Kash.) (*Tatarskie otlozheniya ...,* 2001). The lower boundary of the bed is sharp, 0.65 m thick.

22. Gray, light brown–gray siltstone, undulating laminated, with desiccation cracks, with remains of the plants *Tatarina* sp., *Permotheca* sp., *Phyllododerma* sp., *Taeniopteris* (?) sp., *Samaropsis* sp., *Carpolithes* sp. (*Tatarskie otlozheniya ...,* 2001), 1.1 m thick.

23. Red–dark brown massive clay, 0.2 m thick.

24. Light gray, bluish gray clay, with many thick light brown interbeds in the lower part and spots in the upper part of the bed, fine-undulating laminated, with silty interbeds, 0.65 m thick.

This bed is clearly visible from a distance, and visually traced by me upstream the Sukhona River up to the village of Opoki. 100 m downstream from the site described, it is represented by bluish light gray siltstone, with reddish light brown interbeds and spots, 0.6 m thick. In the area considered, the following beds overlie it:

25. Red–brown clay with greenish gray spots, massive, indistinctly horizontally laminated in the upper part of the bed, slightly silty, calcareous, 1.6 m thick.

26. Gray, horizontally laminated, feldspar–quartz, very fine-grained, thin-platy sandstone, 0.6 m thick.

A more detailed description of Beds 1–26 was provided by Golubev (2000). I studied the overlying deposits in 2001.

27–36. Red-brown siltstone, with beige and gray spots and interbeds and areas and interbeds with dark gray and brown streaks (plant roots), massive or indistinctly horizontally laminated, sandy and clayey, with shells of the ostracodes *Prasuchonella stelmachovi* (Spizh.), *Sinusuella* cf. *ignota* Spizh., *Suchonellina* cf. *futschiki* (Kash.), *S. parallela* Spizh., and *S. spizharskyi* (Posner) (*Tatarskie otlozheniya ...,* 2001). There are interbeds of sandstone (up to 0.4 m thick) and clay (up to 0.4 m thick). Gray, grayish green, beige, light brown, brown sandstone, with vertical, short, light gray streaks (plant roots), horizontally laminated, very fine-grained, friable, with desiccation cracks filled with dark brown clay. Brownish gray and red–brown clay, with indistinct dark gray spots and stains, with short worm-shaped streaks of red–brown (diameter less than 1 mm) and dark gray (more than 1 mm in diameter) color (plant roots), massive, nonplastic, silty, calcareous, with a weak bituminous smell. The middle part of Bed 36 shows channels of even width (up to 8 mm), rounded in cross section, filled with light gray loose sand and outlined by a 2-mm-wide gleization zone of greenish dark brown color. The bed is 3.7 m thick.

37–43. Brown clay with distinct rounded greenish gray spots ("polka dots") up to 2 cm in diameter, with gray worm-shaped streaks of plant roots (interbeds), massive, nonplastic, silty (interbeds), with shells of the ostracodes *Prasuchonella stelmachovi* (Spizh.), *Suchonellina* cf. *futschiki* (Kash.), *S.* ex gr. *parallela* Spizh., *S.* ex gr. *spizharskyi* (Posner), and *S. inornata* var. *macra* (Lun.) (*Tatarskie otlozheniya ...,* 2001), with interbeds (up to 20 cm) of beige, massive, nonplastic clay, 2.6 m thick.

Kichuga Member

44–50. Grayish green clay, with gray and green horizontal streaks of plant roots (up to 1 cm wide, up to three orders of branching), horizontally laminated, nonplastic, calcareous, with interbeds (up to 0.5 m thick) of beige gray, gray–green, undulating laminated, moderately strong, clayey, thinly platy limestone, with subvertical root voids (up to 2 cm in diameter), often filled with green loose clayey mass or calcite crystals; 1.95 m thick.

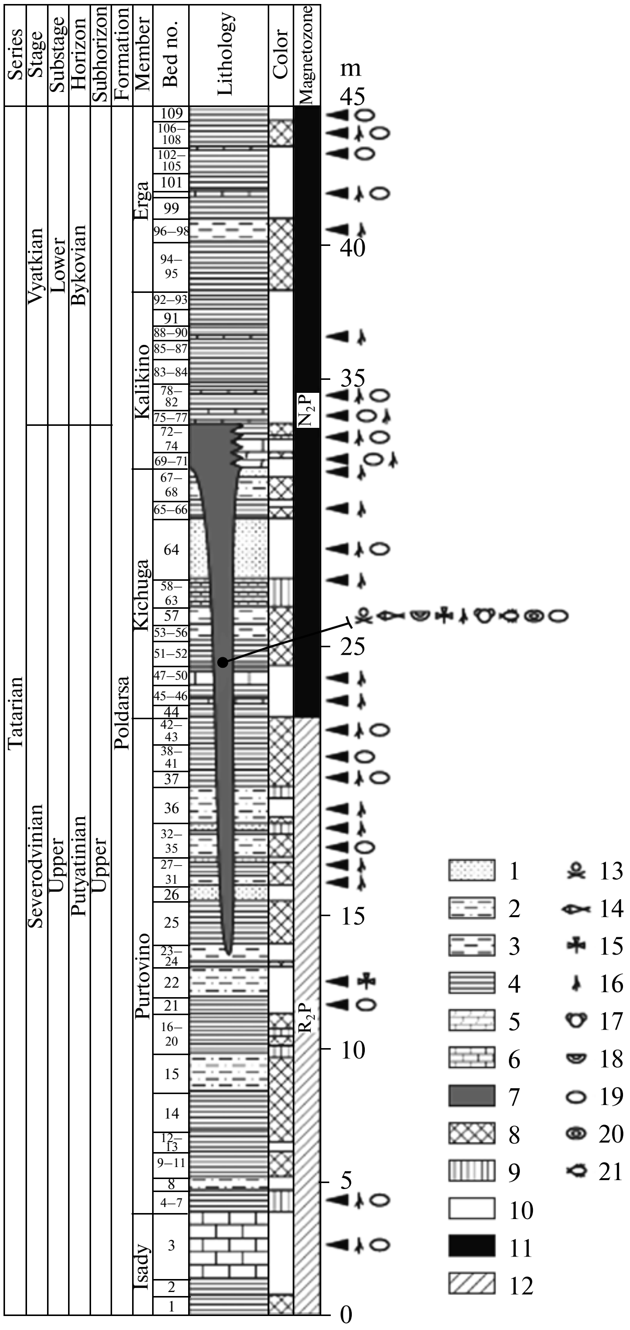

Fig. 3. Geological section of the Upper Permian continental deposits of the Mutovino outcrop, Vologda Region, Russia; Severodvinian. Designations: (1) sand or sandstone; (2) siltstone; (3) clayey siltstone; (4) clay; (5) marl; (6) limestone; (7) rocks of the Mutovino lens; (8) red rocks; (9) speckled rocks; (10) gray rocks; (11) direct polarity; (12) reversed polarity; (13–21) fossils: (13) tetrapods; (14) fish; (15) plants; (16) plant roots; (17) palynomorphs; (18) bivalves; (19) ostracodes; (20) conchostracans; (21) insects.

51–57. Red–brown clay, massive in the lower part and horizontally laminated in the upper part, silty (content of the clastic fraction increases towards the upper boundary of the bed), nonplastic, 2.2 m thick.

58–63. Interbedding clay and sandstone. Red–brown, massive or indistinctly horizontally laminated, unevenly silty and sandy, nonplastic clay, with interbeds with thick gray streaks of plant roots. Gray–green, horizontally laminated, very fine-grained, oligomictic, friable sandstone. The bed is 1.05 m thick.

64. Gray–green, massive to thinly laminated and gently cross-laminated, very fine- to fine-grained, oligomictic, friable sandstone, with fossil bivalves and ostracodes *Prasuchonella stelmachovi* (Spizh.) and *Suchonellina inornata* var. *macra* (Lun.) (*Tatarskie otlozheniya ...,* 2001). Interbeds are of stronger, platy sandstone, with many fine root voids (less than 1 mm in diameter). Some interbeds are several centimeters thick, with interbedding principal rock of the bed and red–brown clay with fine streaks and channels of plant roots. The bed is 2.25 m thick.

65a. Reddish brown clay, with sporadic, fine, short gray streaks of plant roots, indistinctly horizontally laminated, nonplastic, strongly silty, with an interbed (1 cm thick) of grayish green, very fine-grained sandstone, 0.4 m thick.

65b–66. Dark green clay with numerous red spots and, in the upper part, also with fine red worm-shaped streaks of plant roots, massive, nonplastic, silty, with interbeds (up to 4.5 cm thick) of greenish gray, massive, very fine-grained, oligomictic sandstone, 0.3 m thick.

67. Orange red, brownish red, brown, indistinctly undulating–laminated, frail, sandy siltstone, alternating basally with beige very fine-grained sandstone, 0.85 m thick.

68. Sandstone mixed with clay; in the lower part of the bed, gray–light brown; in the upper part gray–green, with primary lamination interrupted by post-sedimentary processes, very fine-grained, with streaks and interbeds of clay, which is dark brown and greenish gray (relicts of the former clayey layers), oligomictic, moderately strong, with beige and gray obscure, poorly visible streaks of plant roots varying in size and thickness, 0.35 m thick.

Kalikino Member

69. Pink–gray, purple gray, brownish gray, massive detrital marl, with well-rounded gravel of dark brown and, considerably less often, greenish dark gray clay, with sporadic horizontal green streaks of plant roots, moderately strong; the lower boundary of the bed is sharp, undulating, 0.15 m thick.

70. Gray detrital marl, with a tinge of purple, massive or with indistinct discontinuous undulate lamination, with rare gravel-scale clasts of dark brown and beige brown marl, with numerous horizontal flat broad clayey streaks (plant roots), moderately strong; the lower boundary of the bed is sharp, undulate, 0.2 m thick.

71. Pink–brown marl, with beige brown and dark brown mainly horizontal streaks of plant roots, indistinctly horizontally laminated, unevenly calcareous (in some areas, with transitions into pink–dark brown clay; with the carbonate content increasing upward in the section), moderately strong, with fossil ostracodes; the lower boundary of the bed is hardly visible, drawn across the line where underlying rocks of fragmentary texture disappear; 0.25 m thick.

72. Purple gray, undulating laminated, unevenly clayey limestone, with fossil ostracodes; in some areas, strongly clayey, gray–purple, undulating laminated, frail, can be crumbled by hand; in some areas, mostly in the upper part of the bed, weakly clayey, gray, massive, very strong, with fine vertical root voids. The lower boundary of the bed is gradual; the bed is 0.45 m thick.

73. Gray–dark brown, brown–gray, dark gray, red–brown (colors with irregularly sharp gradual transitions between them, giving the rock a pale, not bright, unclear aspect), massive, nonplastic clay, with a dense network of fine beige streaks of plant roots and thick (up to 2 mm) vertical root voids, filled with a bright green loose clayey mass, with fossil ostracodes and charophytes. The lower boundary of the bed is indistinct; the bed is 0.15 m thick.

74. Brown clay with greenish dark gray large (centimeter-scale to decimeter-scale) shapeless inexpressive pale spots, with massive, silty, nonplastic streaks formed by plant roots (vertical: bright brown, fine, long; horizontal: brown and grayish green). At the base of the bed, clay is gray–green. The lower boundary of the bed is moderately expressed, with parting; the bed is 0.45 m thick.

Beds 71–74 have yielded the ostracodes *Prasuchonella stelmachovi* (Spizh.) and *P.* ex gr. *stelmachovi* (Spizh.) (*Tatarskie otlozheniya ...,* 2001).

75–82. Interbedding limestone and clay. Limestone is gray, with a greenish tinge, with green horizontal streaks of plant roots, with fine dark green clayey interbeds, massive or undulating laminated, clayey, with horizontal and vertical weakly tortuous root voids (up to 4 mm in diameter), moderately strong, with the fossil ostracodes *Darwinuloides svijazhicus* (Sharap.), *Prasuchonella* ex gr. *stelmachovi* (Spizh.), *Sinusuella vjatkensis* (Posner), *Suchonella blomi* Molost., *Suchonellina* cf. *parallela* Spizh., and *S. inornata* (Spizh.) (*Tatarskie otlozheniya ...,* 2001). Greenish gray clay, with horizontal brown and green, undulating laminated, unevenly calcareous (in some areas with transition to marl), nonplastic, silty streaks of plant roots. The bed is 1.25 m thick.

83–90. Gray, greenish gray clay, with purple gray, thin-horizontally laminated (seasonal) or massive (in the lower part of the rock matter), nonplastic, calcareous, silty to a varying extent (non-silty interbeds are darker) interbeds. The upper part contains a greenish gray, horizontally laminated marl layer (14 cm thick), with a varying extent of carbonate content (from calcareous clay below to clayey limestone above), with small (millimeter-scale) caverns and subvertical channels (up to 9 mm in diameter, on average 4–5 mm) formed by plant roots, confined to the upper, more calcareous part of the bed. The bed roof contains greenish gray, massive, very fine-grained, oligomictic sand (10 cm thick). The bed is 2.2 m thick.

91–93. Green–gray clay, with cyclic stripes. In cyclites, colors replace each other upward in the section as follows: light gray, beige, greenish gray, gray–green, dark gray, greenish dark gray. The transition from light to darker types of clay (within each cyclite) is extremely gradual, while the transition from dark to light types (boundaries between cyclites) is sharp. The cyclites are 1–40 mm thick, on average 3–4 mm thick. Clay ranges from pure (dark interbeds) to strongly sandy–silty (light interbeds), calcareous, nonplastic. In the upper part of the strata, the tinge of green in dark interbeds is gradually replaced by tinge of brown, and desiccation crack appear. The bed is 1.3 m thick.

Erga Member

94–95. Brown, horizontally laminated, silty, nonplastic clay similar in structure to beds 91–93. The proportion of gray layers decreases upward in the section; the lamination becomes thicker and discontinuous; in some interbeds the rock looks massive; the number of desiccation cracks increases. Dark brown, regularly circular spots 5–8 mm in diameter frequently occur on the surfaces of layers; they are distinctly visible against the beige background of the base rock, but are usually impossible to trace deep into the rock. The lower boundary is unsharp; the bed is 1.8 m thick.

96–98. Orange brown, massive, nonplastic, strongly silty clay, interbeds with lighter streaks around fine (less than 1 mm in diameter) channels (? plant roots), at the base and at the top with a transition to clayey siltstone. The lower boundary is sharp; the bed is 0.85 m thick.

99. Greenish gray clay, with a tinge of brownish in the lower part of the bed, with fine (less than 1 mm), short (one or several centimeters) horizontal weakly wavy brown–red streaks, very indistinct thin-undulating laminated, almost massive, almost nonsilty, calcareous. The bed is 0.8 m thick.

100. Dark gray, massive limestone, in places, with relict discontinuous horizontal undulating lamination, strong, with fossil ostracodes, with root voids, which are filled with a greenish beige loose clayey matter. At the top of the bed, clayey, not strong, loose, platy. The lower boundary of the bed is indistinct; the bed is 0.22 m thick.

101. Gray–green clay, with brownish spots and interbeds, horizontally laminated (as in bed 91, but bedding is less pronounced and often discontinuous), silty to a varying extent; in the lower part of the bed (20 cm thick), with interbeds with fine marl gravel; the bed is 0.7 m thick.

102–105. Gray clay with a tinge of greenish, with red, fine intertwining , massive, nonplastic, calcareous streaks. The bed is 0.95 m thick.

106–108. Red–brown clay, with small, short tortuous beige streaks of plant roots in the upper part, massive, nonplastic, with silty interbeds, with fossil ostracodes. The bed is 0.95 m thick.

109. Gray–green, horizontal laminated clay, with interbeds of light gray very fine-grained sand and green–gray clay, with large brown spots. The rocks are strongly weathered. Exposed thickness is 0.6 m.

Further upwards, to the bank line, the area is soddy; 3 m of thickness.

Geology of the Mutovino Lens

The Mutovino lens is located more than 300 m upstream from the above-described outcrop, in the middle part of the riverbank slope. It is clearly visible from a distance, standing out against the bluish gray–red banded background of the enclosing deposits by its speckled, mostly dark gray coloration. The gray color is a prominent feature of this lens, distinguishing it from all other large Permian lenses of the Sukhona and Northern Dvina rivers, which usually have yellow–brown coloration.[2] The Mutovino lens is formed mostly by not strong rocks; as a result, most of the lens is poorly denuded: covered with screes or hidden under dense tree and shrub vegetation. The boundaries of the lens are also hardly visible. It is undoubtedly asymmetrical: the western basal part, which is positioned upstream the river, is gently sloping; the eastern part is steeper; the ratio of the distances from the point of the maximum thickness of the lens to its western and eastern edges is 3 : 1. At the level of its maximum thickness, the lens cuts into the underlying deposits to Bed 24; its base is located 9.6 m higher than the top of the limestone of Bed 3. The deposits overlying the lens begin with Bed 75 (lower beds are indistinguishable; they are either absent or facially changed); thus, the maximum thickness of the length is 20 m. The position of the edges of the lens could not be determined precisely; therefore, the length of the lens was estimated approximately as at least 200 m.

The lens is complex in structure. It is formed mostly of fine-texture matter: clay, siltstone (prevailing), and very fine- to fine-grained sandstone. The deposits are speckled. Red and brown rocks are rare, represented mostly by clays. Yellow formations, siltstones and conglomerates, are much more widespread; and gray deposits prevail.

In the lower part of the lens, the rock is coarser, composed mostly of siltstone, sandstone, gravelites, and conglomerates. Gravelites and conglomerates are

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[2] Gray color characterizes many “small” (one or a few meters thick and one or several dozen meters long) clayey–sandy lenses of the Poldarsa Formation: Poteryakha-2, Kochevala-1, Navoloki, Ust’e Strel’ny, and others (Golubev, 2000).

mostly well-rounded gravel and pebbles of green clay and carbonized wood fragments in the matrix of yellow or gray siltstone. All rocks are strongly carbonaceous and usually contain scattered fish and tetrapod bones and bivalve and ostracode shells. The lamination is horizontal or oblique; the prevailing dip azimuth of the oblique laminae are 0°–20° (Verzilin et al., 1993). The clastic fraction is composed mostly of quartz (85%), with an admixture of feldspars (10%). The principal minerals in the heavy fraction are garnets of the pyrope–almandine group (68%), epidote (9%), ilmenite (3.1%), staurolite (2.9%), and tourmaline (2.8%); some samples contain rather large amount of biotite (25.5%); visible amounts of other minerals include hematite and magnetite (0.9%), rutile (1.1%), and chrompicotite (chrome spinellides) (1.6%) (Verzilin et al., 1993).

The upper part of the lens is formed of siltstones and clays gray, brown-gray, brown, horizontally laminated, containing fossil plant remains, bivalves, insects, ostracodes, and conchostracans.

Paleontology

The rocks of the Mutovino lens are literally saturated with extremely diverse fossils. The most notable are plants and vertebrates.

Fossilized plant remains found in the locality are dominated by shoots of the conifers *Quadrocladus schweitzeri* Meyen in association with strobili of *Dvinostrobus sagittalis* Gomankov et Meyen. The subdominant fossils are leaves of the peltasperm pteridosperm *Tatarina conspicua* Gomankov et Meyen in association with peltate ovuliphores of *Peltaspermopsis* cf. *buevichae* Gomankov et Meyen, seeds of *Salpingocarpus bicornutus* Meyen, *S. variabilis* Meyen, and sporangia of *Permotheca striatifera* Meyen et Gomankov and *P. vesicasporoides* Meyen, Esaulova et Gomankov. There are also abundant fossilized leaves of the cardiolepids *Phylladoderma* (subgenus *Aequistomia*) *annulata* Meyen, *P.* (*A.*) *rastorguevii* Meyen, and *P.* (*A.*) *trichophora* Meyen. In addition, Gomankov and Meyen (1986) reported on leaves of the *Rhaphidopteris* type and fragments of the leaves of uncertain systematic position *Arisada densa* Meyen. Spore-bearing plants are represented by leaves and megaspores of the lycapod *Lepidophylloides delicata* Gomankov. Other fossil plants found in the Isady locality include leaves with venation of the *Taeniopteris* type, which Gomankov (Gomankov and Meyen, 1986) assigned to a new fern genus, *Fefilopteris* Gomankov (list prepared by E.V. Karasev, PIN).

Abundant fish bones belong to *Isadia sukhonensis* A. Minich, (?) *I. aristoviensis* A. Minich, *Isadia* sp., *Geryonichthys longus* A. Minich, *Geryonichthys* sp., *Mutovinia stella* Minich, *Strelnia certa* A. Minich, *Toyemia tverdochlebovi* Minich, and Actinopterygii ordo indet. (*Tatarskie otlozheniya ...,* 2001).

The tetrapod oryctocoenosis is represented exclusively by aquatic and subaquatic forms. The dominant fossils are the chroniosuchid anthracosaur *Chroniosaurus levis* Golubev (63%). Somewhat less abundant are the temnospondyl *Dvinosaurus primus* Amalitzky (26%). The kotlassiomorphs *Microphon* sp. and *Microphon arcanus* Bulanov occur less frequently (8%). The predatory therapsid Gorgonopidae gen. indet. (2%) and large phytophagous parareptile Pareiasauridae gen. indet. (1%) are represented by isolated specimens.

Fossil ostracodes are usually poorly preserved. According to I.I. Molostovskaya, the assemblage includes the following forms: *Prasuchonella stelmachovi* (Spizh.), *P.* ex gr. *stelmachovi* (Spizh.), *Sinusuella ignota* Spizh., *S. vjatkensis* (Posner), *Suchonellina inornata* Spizh., *S. inornata* var. *macra* (Lun.), *S. parallela* Spizh., *S. parallela* var. *typica* (Lun.), *S. undulata* (Misch.), *S.* ex gr. *futschiki* (Kash.), and *S.* ex gr. *spizharskyi* (Posner) (*Tatarskie otlozheniya ...,* 2001). In the summer of 2009, the Geological and Paleontological Expedition of the St. Alexius Hermitage (Pereslavskii District, Yaroslavl Region) headed by M.P. Arefiev collected mudstones containing abundant plant remains in the middle part of the lens. Ostracodes were washed out of the samples and analyzed by D.A. Kukhtinov (Lower Volga Research Institute of Geology and Geophysics, Saratov). The assemblage is represented by abundant, mostly strongly distorted valves, shells, and sometimes also internal molds of the ostracode species *Suchonellina inornata* Spizh., *S. parallela* Spizh., *S. perlonga* (Sharap.), *Suchonellina* sp., *Prasuchonella nugushensis* (Kotsch.), *Sinusuella ignota* Spizh., and *Darwinuloides tataricus* Posner; according to I.I. Molostovkaya, the last species is a younger individual of *D. svijazhicus* (Sharap.).

The insect assemblage is particularly diverse. To date, the insects described and reported from this locality include members of 69 families, 81 genera, and 105 species, representing 25 orders (see Chapter 1.2.3).

Numerous fossil conchostracans and the bivalves *Palaeomutela subparallela* Amalitzky, *P. verneuili* (Amalitzky), *P. semilunulata* Amalitzky, *Palaeanodonta novoculchumica* (Kuloeva), *P.* ex gr. *trapezoidalis* (Amalitzky), *Opokiella tschernyschewi* Plotnikov (list from *Tatarskie otlozheniya ...,* 2001, edited by V.V. Silantiev, Kazan [Volga Region] Federal University, Kazan). The *Palaeomutela* species found in Mutovino are typical of the so-called “Doskino association” (Gusev, 1990).

Stratigraphy

The Mutovino section characterizes the middle part of the Poldarsa Formation. Exposed strata include the Isady (upper part), Purtovino, Kichuga, Kalikino, and Erga (lower part) members (Fig. 3). The lower, larger part of the section (Beds 1–43) is characterized by the Late Severodvinian (Putyatinian) ostracode assemblage of the *Suchonellina inornata—Prasuchonella stelmachovi* Zone: *Suchonellina inornata* Spizh., *S. inornata* var. *macra* (Lun.), *S. parallela* Spizh., *S. parallela* var. *typica* (Lun.), *S. spizharskyi* (Posner), *S. futschiki* (Kash.), *Prasuchonella stelmachovi* (Spizh.), and *Sinusuella ignota* Spizh. The upper part of the section (Beds 75–109) is characterized by the Early Vyatkian (Bykovian) ostracode assemblage of the *Wjatkellina fragilina—Dvinella cyrta* Zone: *Sinusuella vjatkensis* (Posner), *Darwinuloides svijazhicus* (Sharap.), *Suchonella blomi* Molost., *S.* ex gr. *blomi* Molost., *Suchonellina futschiki* (Kash.), *S. inornata* (Spizh.), *S. inornata* var. *macra* (Lun.), *S. parallela* Spizh., *S. spizharskyi* (Posner), *S. parallela* var. *typica* (Lun.), *S. undulata* (Misch.), *Wjatkellina vladimirinae* (Bel.), *W.* sp., and *Prasuchonella* ex gr. *stelmachovi* (Spizh.) (*Tatarskie otlozheniya ...,* 2001). The presence in Beds 75—77 of the ostracodes *Darwinuloides svijazhicus* (Sharap.) and *Suchonella blomi* Molost. and the absence of them, as well as other typically Vyatkian forms in the lower deposits allowed fixing the lower boundary of the Vyatkian Stage in this section at the base of this bed (Commission for the Permian System ..., 2006). It is proposed to fix the lower boundary of the Bykovian Horizon at the same level. But it should be noted that typically Severodvinian ostracodes are absent in Beds 44-74, and age of these beds is uncertain. That's why a detailed study of the boundary beds of the Mutovino section, with precise fixation of the lower boundary of the Vyatkian Stage is among the most important and urgent problems of the Permian stratigraphy.

It is difficult to determine the upper boundary of the lens itself, because it is only poorly denuded. It was previously believed that the lens was confined to the Purtovino Member, or member "b" in the chart by the Saratov geologists cited (Pakhtusova in Golubev, 2000; Molostovski et al., 1979; Strok and Buslovich, 1979; *Opornyi razrez ...,* 1981; Gomankov and Meyen, 1986; Gomankov, 1997). Subsequently, many specialists came to the conclusion that the upper boundary of the lens was positioned higher than the top of the Purtovino Member, in the lowermost part of the member "c" in the chart of the Saratov geologists, or in the Kichuga Member (Verzilin et al., 1993; Golubev, 2000; *Tatarskie otlozheniya ...,* 2001). However, my study performed in 2001 showed that the cut is positioned even higher, in the lowermost part of the Kalikino Member, within Beds 69–74. Consequently, according to geological data, the top of the lens is positioned lower than the supposed lower boundary of the Vyatkian Stage and the Bykovian Horizon (base of Bed 75; Fig. 3). This conclusion is confirmed by the data on ostracodes. According to D.A. Kukhtinov, the mudstones of the lens belong to the Severodvinian Stage, probably to its upper part. Thus, the stratigraphic position of the Mutovino lens can currently be identified as the terminal part of the Upper Severodvinian Substage (the upper part of the Upper Putyatinian Subhorizon).

According to paleomagnetic data, the locality is positioned in the lower part of the normal polarity magnetozone N_2P. The data on vertebrates allow identifying unambiguously the position of the lens within the *Toyemia tverdochlebovi—Mutovinia stella* Ichthyozone and the *Chroniosaurus levis* Tetrapod Subzone of the *Proelginia permiana* Zone. This tetrapod subzone characterizes the Upper Severodvinian—Lower Vyatkian boundary beds (Upper Putyatinian—Bykovian); the fish zone comprises Upper Severodvinian (Upper Putyatinian) deposits (Fig. 4).

Conditions of the Formation of the Mutovino Lens

The Mutovino section has a structure typical of the Poldarsa Formation, which is on the whole characterized by a frequent alternation of clayey—carbonate rocks with a smaller amount of fine-grained clastic rocks (Golubev, 2000). The elementary beds recognized within this formation are usually relatively thin (on average 0.4 m thick) and spread over many kilometers. This kind of structure distinguishes deposits of large basins with an unstable sedimentation regime. In the case in question, it was a lake and vast adjacent alluvial lowland with the dissected relief. Lake deposits are represented by gray clayey—carbonate rocks; alluvial deposits, by red silty—clayey (floodplain alluvium) and, less often, sandy (stream channel alluvium) deposits. The Poldarsa Formation does not include localities with undoubtedly terrestrial tetrapods. All oryctocoenoses of this formation are dominated by aquatic forms: chroniosuchids, dvinosaurs, and kotlassiomorphs; such amphibionts as pareiasaurs or gorgonopids are considerably less frequent. Fossils of the most terrestrial tetrapods, such as dicynodonts, have not been found in the Poldarsa Formation. Thus, the Poldarsa Formation was formed under conditions of a strongly watered alluvial—lacustrine plain.

The morphology of the Mutovino lens, the presence in its composition of deposits with oblique bedding suggest that this geological body was formed by a stream. The great thickness of the lens, prevalence of fine, clayey—silty deposits in its composition, absence of thick oblique series and predominance of deposits with horizontal lamination, abundance of fossil plant remains, insects, and aquatic tetrapods are evidence that the deposits were formed in the terminal, mouth part of the river, rather than in the stream channel. Judging from the prevailing dip azimuth of oblique layers, the water masses in the Mutovino area flew north-northeasterly. However, it would be wrong to assume that the river also flew precisely in that direction, and its source lay south-southwest of the locality. The high extent of maturation of clastic rocks, abundance of garnet in the heavy fraction, and negligibly small admixture of epidote suggest that drifting terrigenous matter was transported from the Baltic Shield

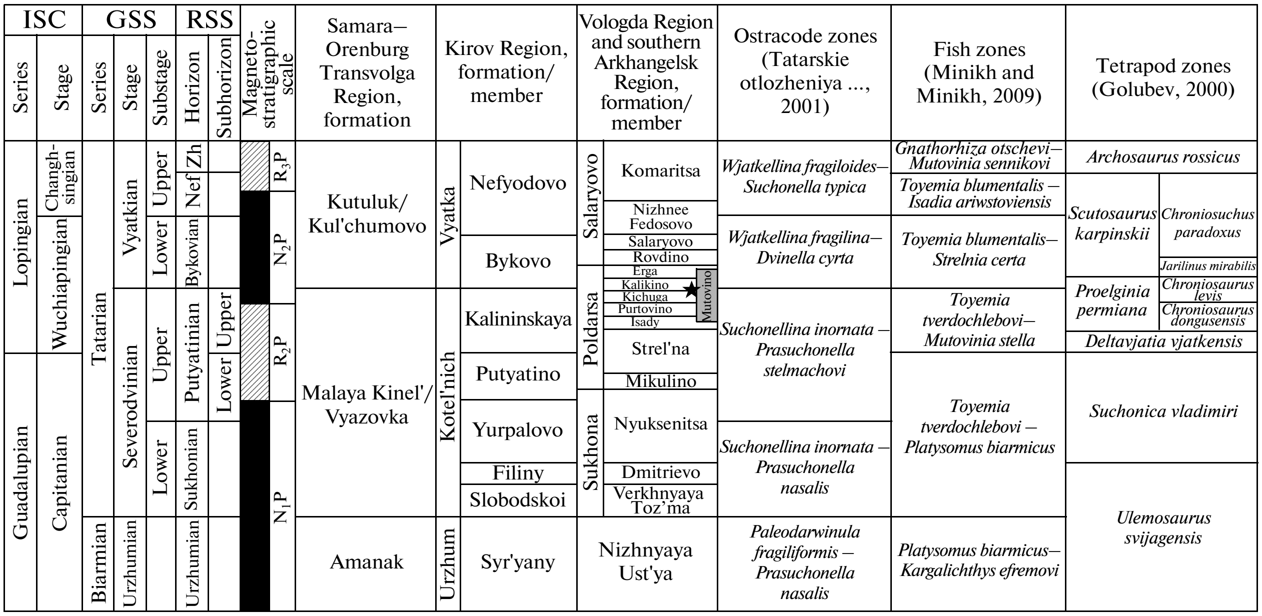

Fig. 4. Stratigraphic scheme of the Upper Permian deposits of European Russia. Asterisk indicates the stratigraphic position of the Mutovino (=Isady) locality, Vologda Region; Severodvinian Stage; gray area indicates stratigraphic units corresponding to the Mutovino section. Designations: (ISC) International Stratigraphic Chart; (GSS) General Stratigraphic Scale; (RSS) Regional Stratigraphic Scale; (Nef) Nefedovian; (Zh.) Zhukovian.

(Strok and Trofimova, 1976). Hence, the river flew from the Baltic Region, i.e., from the northwest. Perhaps, the mismatch between the general direction of the river and direction of the Mutovino flow is accounted for by the formation of the Mutovino lens in the left marginal part of the river delta rather than in its axial zone.

Conclusions

Mutovino is one of the richest localities of Late Permian nonmarine organisms in European Russia. Fossils found here include abundant plant remains (15 forms), bivalves (six forms), insects (at least 102 forms), ostracodes (14 forms), conchostracans, fishes (at least seven forms), and tetrapods (five forms). The locality is represented by an asymmetrical lens formed by gray clayey–silty deposits of alluvial origin. The Mutovino lens is positioned in the lower part of the Kalikino Member of the Poldarsa Formation, in the uppermost part of the Upper Severodvinian Substage (Putyatinian Horizon), near its boundary with the Vyatkian Stage (Bykovian Horizon), in the lower part of direct polarity magnetozone N_2P, within the *Toyemia tverdochlebovi–Mutovinia stella* Ichthyozone and *Proelginia permiana* Tetrapod Zone (*Chroniosaurus levis* Subzone). The locality was formed in the marginal part of the delta of a river originating on the Baltic Shield and flowing into a large lake located in the northeastern part of the Moscow Syneclise.

1.2.3. Review of the Entomofauna

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This review covers only a part (although substantial) of the collection of Upper Permian fossil insects from the Isady locality stored in PIN. Since insect-collecting in Isady is very intense and the rate of annual arrival of new material is higher than the rate of its processing and study, we had to restrict ourselves to the part of the collection formed in the period up to 2011. The material collected during the summer of 2011 (around 1000 insect specimens) is mostly unprocessed and excluded from calculations, although some specimens are identified and included in the total systematic list. The studied part of the collection includes about 2500 specimens attributed to 25 orders. To date, the materials described or identified represent 69 families, 81 genera, and 105 species, including 24 genera and 78 species described as new. The complete systematic list of insects is given at the end of this chapter. In addition to insects, the fossils found in Isady include rather infrequent remains of the cuticle of scorpions (Fet et al., 2011) and one fossil centipede (Chilopoda). The uniquely high richness and diversity of the entomofauna make Isady the first among all known Late Permian localities. The only

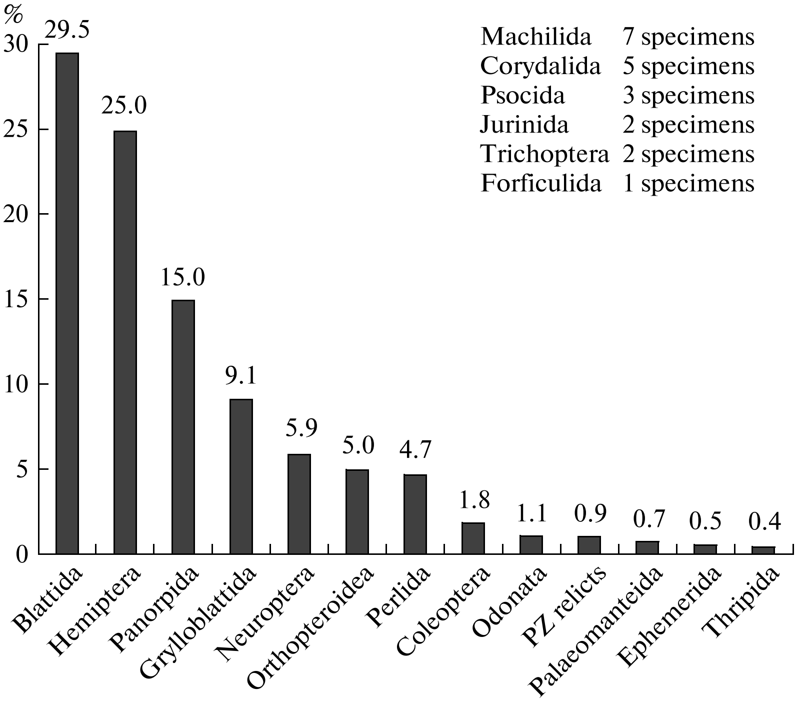

Fig. 5. Distribution of insects over different orders in the Isady locality, Severodvinian Stage of the Vologda Region.

collection comparable in size is known from the Lower Changhsingian (Shi et al., 2010) Belmont locality in Australia (New South Wales, Upper Newcastle Coal Measures at Belmont and Warner's Bay area north of Sydney; Croudace Bay Formation, Belmont Conglomerate Member). The collection from this locality includes about 3000 specimens, some of which are parts and counterparts marked with different numbers (Beattie, 2007). Members of 35 families are known from Belmont (see Chapter 3.1).

The extent to which insects of different orders have been studied is extremely uneven. Some orders, including Grylloblattida, Perlida, Coleoptera, and Panorpida, have been studied in detail, while two others, namely, Hemiptera and Blattida, remain almost unstudied, although they are among the most abundant and diverse orders. Most of the neuropterans, some orthopteroids, and several small groups, such as Psocida, Thripida: Lophioneuridae, Protelytroptera, and Parasialidae, have not been treated. Representatives of these groups are only preliminary identified (to family) wherever possible.

Among fossil insects unrelated to the aquatic environment, Blattida and Hemiptera are most abundant (Fig. 5). This composition of dominants is common to most of the Middle and Late Permian insect assemblages of European Russia (Shcherbakov, 2008). The subdominants are Panorpida and Grylloblattida. A little less abundant are Neuroptera and, even less so, Orthoptera. Considerably less abundant orders include Coleoptera, Odonata, Palaeomanteida, Phasmatida, and, possibly, ?Mesotitanida. The rarest groups in Isady include Psocida, Thripida: Lophioneuridae, Corydalida (=Megaloptera), Trichoptera, and Jurinida (=Glosselytrodea), as well as orders relict for the Late Permian: Dictyoneurida, Mischopterida, Caloneurida, Eoblattida, and Hypoperlida (both Hypoperlina and Strephocladina). The total number of specimens of the last five orders is at most 1% of the total number of insects.

Amphibiotic insects are represented mostly by stoneflies (Perlida); mayflies (Ephemerida) are much less abundant. The order Perlida is represented by a substantial number of various wings of adults and numerous fossil nymphs. The latter have not been taken into account in calculations of the percentages of insect orders, because both fossil nymphs themselves and fossil remains of their exuviae are represented by hundreds of specimens and sometimes cover whole bed surfaces. Mayflies are rather infrequent and represented mostly by wings of adults; a single aquatic mayfly nymph has also been found. Some schizophoroid coleopterans and dasyleptids probably also had aquatic or amphibiotic modes of life. Pre-adult stages of Odonata and Trichoptera have not been found.

Preliminary calculations of the percentages of orders (not taking aquatic nymphs into account) are shown in Fig. 5. The values given are extremely approximate, because the materials collected have not been fully processed and some bed surfaces are saturated with numerous wing pieces that could not be counted. In addition, some groups have prominent distinguishing characters, such as the characteristic intercalary veins of cockroaches and the dense, coriaceous, often sculptured membranes of homopterans, which allow identifying the members of respective orders even from extremely small wing fragments. This factor also garbles the results of calculation of the relative abundance of different groups in the oryctocoenosis.

A brief review of some orders is given below, according to their proportions in the entomofauna. We had to refrain from analyzing such abundant and diverse groups as Blattida, Hemiptera, and Neuroptera, because they have been studied insufficiently. A review of Coleoptera of Isady is given separately, in Chapter 2.2.3.

Mayflies (Ephemerida). About ten mayfly specimens have been found in Isady, all are represented by wing fragments. Four of them belong to Protereismatidae Sellards, 1907 and two to Misthodotidae Tillyard, 1932, the primitive families which had almost homonomous wings.

Previously, members of Protereismatidae have only been found in deposits earlier than the insect-bearing beds of Isady. Until recently, the family Protereismatidae included one genus, *Protereisma* Sellards, 1907, three species of which were described from adults from the Lower Permian of Kansas (Elmo locality), USA, and one was described from nymphs from the Lower Permian of Moravia (Obora locality), Czech Republic. The genus *Alexandrinia* Sinitshenkova et Vassilenko, 2012 was established based on two specimens (large wings) from Isady, with the type species *A. gigantea* Sinitshenkova et Vassilenko, 2012. The species originally described as *P. directum* Carpenter, 1979 from the Lower Permian of Oklahoma is also assigned to this genus. Undescribed fossils from Isady include another specimen that undoubtedly belongs to the genus *Alexandrinia,* but is considerably smaller in size than *A. gigantea* (Sinitshenkova and Vassilenko, 2012). One more member of this family *Ponalex maximus* Sinitshenkova et Aristov, 2012 is the largest among all known true mayflies (Sinitshenkova and Aristov, 2012).

The family Misthodotidae, which includes two genera and ten species, is the only mayfly family that crossed the Permian–Triassic boundary. It is known from Lower Permian deposits of North America, Western Europe, and the Perm Region of Russia and from the Middle Triassic of Western Europe. Several wing fragments have been found in Isady, identified as *Misthodotes tshernovae* Sinitshenkova et Vassilenko, 2012 (Sinitshenkova and Vassilenko, 2012). The second species of this family will be published in the near future.

The only small nymph identified as a mayfly (PIN, no. 3840/1167, with the body about 1 cm long) shows long hindwing primordia, long pointed processes on posterolateral angles of abdominal tergites, and, possibly, small lamellate gills with a fringe of branchial filaments and the base of one cercus. The unsatisfactory preservation of this specimen prevents more precise identification.

Dragonflies (Odonata). Fossil dragonflies are not numerous in Isady, but have been found rather regularly. To date (taking into account the materials collected in 2011), 35 dragonfly specimens are known from the Isady locality. The dragonfly assemblage is endemic at the generic level and occupies a special place among the known Late Permian faunas. Members of the family Kennedyidae, known from Lower Permian deposits of the United States (Kansas, Oklahoma) and Russia (Chekarda, Kungurian Stage), the Middle Permian of Russia (Soyana, Kazanian Stage), and the Triassic of Kyrgyzstan (Madygen, Ladinian–Carnian), are dominant. Only six genera with a few species have been described to date in the family Kennedyidae, while the material from Isady, which remains undescribed, belongs to at least five new genera. Members of the family Permolestidae are also rather diverse, but relatively infrequent; however, this family is represented in the material by small wing fragments. Meganeuridae, Ditaxineuridae, and Permaeschnidae, typical of the Permian and usually abundant, have not been found in Isady; the same concerns clearly Triassic forms of Odonata.

All dragonflies found in Isady belong to moderately and poorly flying forms and have adaptations to maneuvering among dense vegetation (petiolate wings). A rather high diversity combined with the absence of perfectly flying Meganeuridae and Permaeschnidae is probably attributable to ecological factors.

The relatively large wings of Permolestidae are strongly fragmented, which can be explained by a long transportation to the locality where they became fossilized. At the same times, the preservation of small forms (all of them belong to the family Kennedyidae), i.e., the presence of complete wings and, in one case, a complete insect, suggests transportation of remains for a short distance, if at all. It seems plausible that kennedyids lived among dense vegetation in the vicinity of the Isady water body.

Palaeomanteida are relatively rare, but rather diverse and represented by three families: Permosialidae, Palaeomanteidae, and Permembiidae (the system of the order accepted here is discussed in Chapter 2.1.). Three specimens are described in Permosialidae, the typical Permian genus *Epimastax*. One specimen is provisionally referred to the genus *Tridelopterum* (Palaeomanteidae), which is known from the Carboniferous–Permian boundary beds (Rasnitsyn et al., 2004). Two new genera are established based on two more fossil palaeomanteids: *Issapaloptera* gen. nov. and *Neembia* gen. nov., and assigned to the predominantly Early and Middle Permian family Permembiidae, which is, thus, recorded for the first time in the Late Permian.

Jurinida, or Glosselytrodea, are among the rarest orders in Isady. The collection includes only two wings, representing two new species; one proved to be a member of a new genus, *Issadella* gen. nov. of the family Jurinidae; the other has provisionally been referred to the genus *?Karajurina* of the family Glosselytridae (for more detail, see Chapter 2.1).

Scorpionflies (Panorpida = Mecoptera). Scorpionflies in Isady are subdominants, being the third most abundant order after Blattida and Hemiptera. They are represented by Permochoristidae (209 specimens, about 68%), Mesopsychidae (64 specimens, about 21%), and the recently described Nedubroviidae (33 specimens, about 10%), which compose the core of the fauna as well as by sporadic records of Permotanyderidae (two specimens) and Robinjohniidae (one specimen). Among Permochoristidae, three-quarters of specimens belong to the tribe Mesochoristini of the subfamily Permochoristinae: the genera *Tatarakara* Novokshonov, 1995, *Mesochorista* Tillyard, 1916, and *Permeca* Novokshonov, 1995; the most abundant species in Isady is *Tatarakara variomaculata* sp. nov. (over 120 specimens). The other Permochoristidae presumably belong to the tribe Petromanteini: *Neudolbenus* gen. nov. (two species, four specimens) and several other not yet identified genera (about 40 specimens). Three more specimens belong to the same species of the genus *Agetopanorpa,* subfamily Agetopanorpinae, i.e., *A. danili* sp. nov. (see Chapter 2.4).

The Mesopsychidae are represented by a very archaic genus, *Permopsyche* Bashkuev, 2011, which retains some permochoristid features. Two species from the Upper Permian of Australia described in the genus *Mesopanorpodes* have also been transferred to this genus as *Permopsyche belmontensis* (Riek, 1953) and *P. robusta* (Riek, 1953). The Mesopsychidae have long been known only beginning from the Middle Triassic, although recent studies have shown that this family was also widespread in the Late Permian, especially around the Permian–Triassic boundary (Bashkuev, 2011b).

The family Nedubroviidae, represented in Isady by a single species of the genus *Nedubrovia,* is also known from the Permian–Triassic boundary beds of European Russia (Bashkuev, 2011a) and the Tunguska Basin (Bashkuev, 2013).

The generic composition and the dominance of Mesochoristini make the Isady Panorpida assemblage particularly similar to that of the Akkolka Formation of Karaungir (eastern Kazakhstan) (Novokshonov, 1995); however, the Isady fauna appears in general more advanced (the Karaungir Fauna contains a considerable percentage of the Middle Permian forms *Petromantis* and *Asiachorista*: Bashkuev, pers. observ.). In regard to other groups, the mecopteran assemblage of Isady is rather similar to Late Permian Gondwanan faunas: those of the Normandien Formation of KwaZulu-Natal, South Africa (which contains similar species of Agetopanorpa and probably also some Petromanteini) and of Australian Belmont (similar in the presence of Mesopsychidae, Permotanyderidae, and Robinjohniidae). Unfortunately, generic identification of some permochoristids from the Normandien Formation provided by Van Dijk and Geertsema (1999) is questionable and, hence, complicates the classification of related taxa from Isady, especially of Petromanteini. Therefore, some new species have intentionally been omitted from this study; it will be more appropriate to describe them following a reexamination of the material collected in South Africa.

Caddisflies (Trichoptera) belong to the rarest orders in Isady; they are represented by only two impressions. Both belong to the same species of the genus *Cladochorista,* which belongs to the family Cladochoristidae, widespread in the Late Permian and Triassic (for more detail, see Chapter 2.5).

Grylloblattida. Grylloblattids are the most diverse group in Isady. The order is represented by 11 families, 24 genera, and 30 species (see list below), making up about 9% of insect specimens identifiable to order. A total of over 200 fossil grylloblattids have been collected in Isady from 2005 to 2010; 87 of them have been identified to family. The dominant family is Chauliodititidae, followed by the somewhat less abundant Megakhosaridae and Geinitziidae. The families Liomopteridae and Blattogryllidae are rather infrequent; Mesorthopteridae, Permotermopsidae, Cacurgidae, Tunguskapteridae, Kortshakiliidae, and Permulidae occur sporadically (Aristov, 2008a; 2009a; 2012, 2013a; Aristov and Storozhenko, 2011; see also Chapter 2.6).

The qualitative comparison of the grylloblattid fauna of Isady is complicated by its high diversity compared to the relatively low diversity of other Upper Permian faunas. Quantitatively, the Isady Fauna differs from the Upper Permian faunas known outside European Russia primarily by the dominance of Chauliodititidae and the low proportion of Liomopteridae. In the Upper Permian of Angaraland and Gondwana, the latter family is absolutely dominant, and chauliodititids are sporadic or absent. Within European Russia, we have to compare Isady with Vyatkian localities, since the only representative Severodvinian locality of Novo-Aleksandrovka in the Orenburg Region is not sufficiently rich (see Chapter 1.1). The relative proportions of Chauliodititidae and Megakhosaridae make the Isady grylloblattids similar to the Upper Vyatkian fauna of the Sokovka and Balymotikha localities in the Vladimir Region. Isady differs from Balymotikha in the presence of Liomopteridae. Their presence and a high proportion of Megakhosaridae differ Isady from the Permian–Triassic Nedubrovo locality in the Vologda Region. The grylloblattid fauna of Isady is especially similar to that of the Upper Vyatkian fauna of Aristovo in the Vologda Region. The difference of Isady from this locality is the greater proportion of Megakhosaridae (see Chapter 1.3). However, a more objective comparison of the Isady Fauna with those of other localities requires collecting additional material in the mentioned localities.

Stoneflies (Perlida = Plecoptera), one of the most abundant groups in the taphocoenosis of Isady, displaying an extremely high diversity; the assemblage described from this locality is the richest one in the Permian. The core of the assemblage in both abundance and species diversity is formed by Palaeonemouridae (suborder Nemourina), the most abundant family in most of the Permian faunas of Eurasia. A total of 15 species of four genera have been described from Isady, including nine species of the most abundant genus in Isady, *Palaeotaeniopteryx* (seven of them are described in this monograph), and this number is probably far from the actual diversity of Palaeonemouridae in Isady. All species are described based on holotypes or a small type series, and none of them can be called prevailing.

The other stoneflies, which belong to the suborder Perlina, are rather infrequent. Only Palaeoperlidae (three species of the genera *Properla* and *Kargaloperla*) are more or less abundant. Two other families, presumably Gondwanan elements, are represented by only one or two specimens: Eusteniidae (two specimens of *Boreoperlidium borealis* gen. et sp. nov.) and Euxenoperlidae (fragment of a crumpled forewing, supposedly belonging to the genus *Gondwanoperlidium*).

All the above-listed stoneflies have been described from wings. Among nymphs, in spite of their abundance (hundreds of specimens), very few have been preserved sufficiently well for determination. One of these fossils is described here as *Issadoperla permiana* gen. et sp. nov. in the Kungurian family Tshekardoperlidae.

The exceptional diversity of stoneflies in Isady suggests that the taphocoenosis contains elements of biocoenoses that existed in more remote habitats. The stonefly remains were probably transported to the area where they became fossilized by streams from extensive basins. Stonefly nymphs, taking into account the allochtonous character of their preservation, probably lived in the inflowing streams rather than the basin itself (for more detail, see Chapter 2.7.).

Orthopteroid insects (Orthopteroidea), represented by the orders Orthoptera, Phasmatida, and, possibly, Mesotitanida (=Titanoptera), make up about 5% of insects known from the locality. Unfortunately, a large part of specimens are small and poorly informative wing fragments, which cannot be identified even to order, while more complete fossils, suitable for study, have only been processed very selectively. The identified Orthoptera include the families Permelcanidae (subfamily Meselcaninae), Pruvostitidae, and Proparagryllacrididae; one species has been described in each family: *Meselcana vologodica* sp. nov., *Suchonoedischia incompleta* gen. et sp. nov., and *Archifergania issadyensis* gen. et sp. nov., respectively. The presence of Mesozoic elements is remarkable: the genus *Meselcana* has previously been recorded in the Middle to Upper Triassic of Madygen and the Triassic Proparagryllacrididae are found for the first time in the Permian.

In addition to the above-mentioned families, numerous impressions of wings very similar to *Deinotitan orengurgensis* Gorochov, 2007 from the Severodvinian Novo-Aleksandrovka locality, described in the family Mesotitanidae as the earliest member of the suborder Mesotitanina (Gorochov, 2007b), have been found in Isady. The analysis of the venation of these wings, referred to the new genus *Monstrotitan* gen. nov., cast doubt on the assignment of these two genera to Titanoptera. In the present study, both genera are formally referred to Mesotitanida, but it is equally probable that they belong to orthopterans related to Oedischioidea.

The Phasmatida are represented by about ten specimens, based on which three species of the genus *Issadophasma* gen. nov. are described. These forms are probably intermediate between the primitive phasmid *Permophasma kovalevi* Gorochov, 1994 (Permophasmatidae) from the Late Permian Bor-Tologoi locality, Mongolia, and several Triassic Prochresmodidae; they have provisionally been referred to the former family (for more detail, see Chapter 2.8.).

On the whole, families *conditionally considered Paleozoic* dominate in Isady over families *conditionally considered post-Paleozoic*. We consider Paleozoic those families that appeared earlier than the Urzhumian in the Middle Permian and presumably became extinct not later than the Induan in the Lower Triassic. Accordingly, we consider post-Paleozoic those families that appeared not earlier than the Urzhumian and have been found in post-Induan deposits. In addition, we distinguish between transitional families, known from before the Urzhumian and after the Induan, and families conditionally considered endemic to the interval in question, which are not known to occur outside this period. A total of 26 families conditionally considered Paleozoic and 13 families conditionally considered post-Paleozoic are known in Isady. This ratio is typical of Urzhumian and Severodvinian faunas and, to a lesser extent, of later faunas of the Normandien Formation in South Africa and the Sokolova locality in the Kemerovo Region (see Chapter 3.1). The ratio between the numbers of families in the former and latter categories varies among groups. In the infraclass Scarabaeones, the number of families conditionally considered Paleozoic is twice as high as the number of those considered post-Paleozoic, 15 and 7, respectively. Such a high proportion of the former category is largely due to the relatively diverse Paleozoic relicts common in the Late Carboniferous to Early and, partly, Middle Permian. They include four orders with five families: Dictyoneurida (=Palaeodictyoptera), Mischopterida (=Megasecoptera), Caloneurida, and Hypoperlida, the first three of them are recorded in the Upper Permian for the first time. The finds of Dictyoneurida are limited to a single fragment of a nymphal wing, which cannot be identified to genus (Fig. 6a) and probably belongs to the family Calvertiellidae. The only known mischopterid belongs

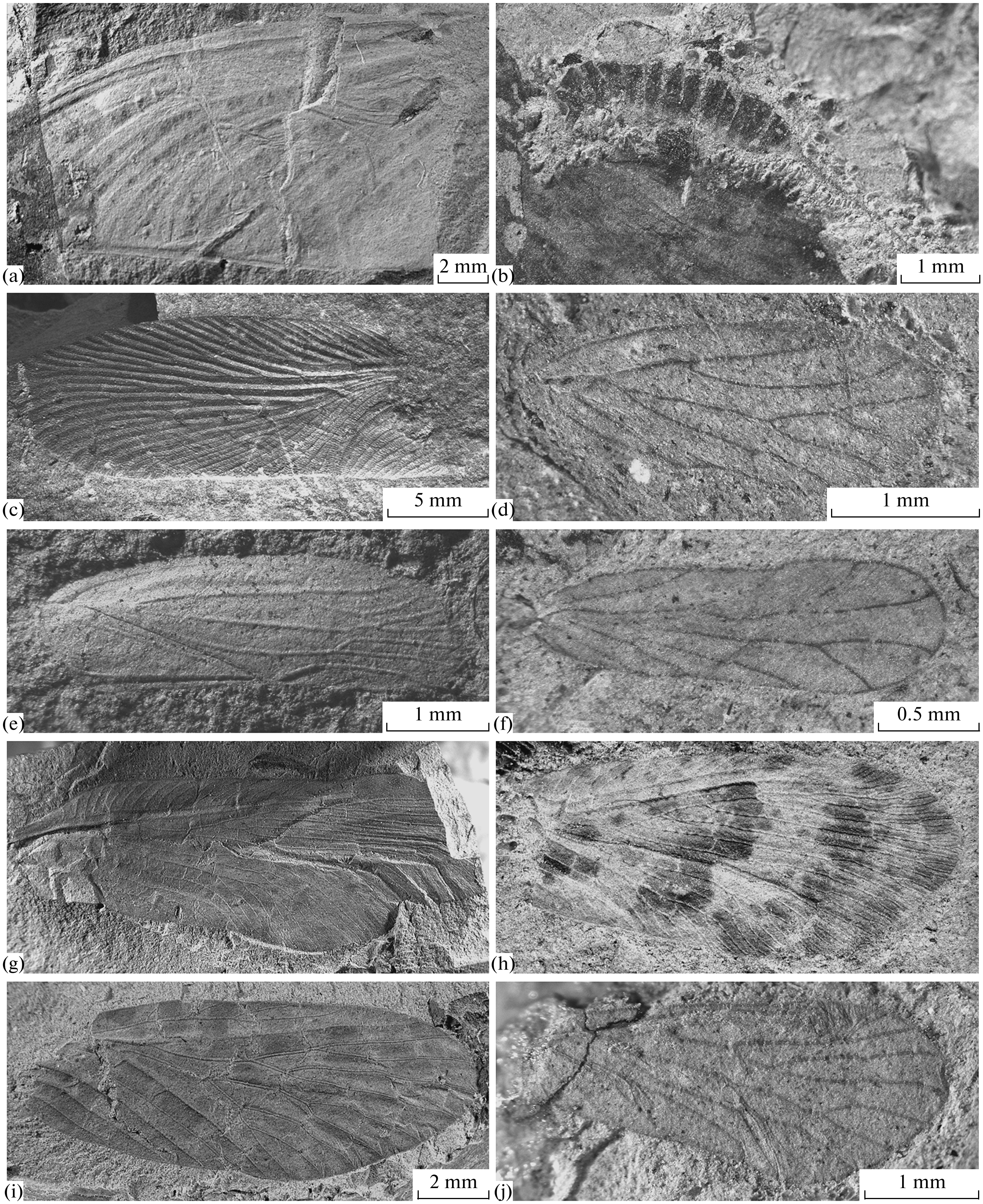

Fig. 6. Undescribed members of different insect orders from the Isady locality, Vologda Region; Severodvinian Stage: (a) Calvertiellidae (Dictyoneurida); (b) Dasyleptidae (Machilida); (c) Phylloblattidae (Blattida); (d) Protopsyllidiidae (Hemiptera); (e) Progonocimicidae (Hemiptera); (f) Lophioneuridae (Thripida); (g) Neuroptera, unidentified family; (h) Permithonidae (Neuroptera); (i) Permochoristidae (Mecoptera); (j) Permotanyderidae (Mecoptera).

to the genus *Issadohymen* gen. nov. of the Early Permian family Moravohymenidae (see Chapter 2.2). Caloneurida and Hypoperlida are more diverse, although they are infrequent and represented together by a total of about twenty impressions. Caloneurida is represented by two species of the new genus *Issadistica* gen. nov. and an undescribed species of the genus *Euthygramma* Martynov 1928 of the family Caloneuridae (see Chapter 2.1). Among Hypoperlida, members of the suborders Strephocladina and Hypoperlina have been described. Strephocladina of the family Ischnoneuridae (=Anthracoptilidae) is represented in Isady by about ten specimens of two species of the endemic genus *Strephoptilus* gen. nov. (see Chapter 2.1.). Prior to these records, the only (and the earliest) Late Permian Strephocladina was described from Belmont (Rasnitsyn and Aristov, 2004). Hypoperlida are much rarer in Isady than Strephocladina and are represented by a single impression identified as a new species of the Early to Middle Permian genus *Idelopsocus* Zalessky, 1929. Note that the material collected in 2011 includes some undescribed Caloneurida and Hypoperlida and the known diversity of these orders is going to increase. Another order that should probably be regarded as a Paleozoic relict is Palaeomanteida, more characteristic of the Early and Middle Permian than of the Triassic. Two of three families of this order (Palaeomanteidae and Permembiidae) found in Isady are conditionally considered Paleozoic; the families considered post-Paleozoic are absent (see Chapter 3.1). Among Ephemerida, members of the Early Permian family Protereismatidae should be regarded as Paleozoic relicts (Sinitshenkova and Aristov, 2012; Sinitshenkova and Vassilenko, 2012); among Odonata, the family Permolestidae is conditionally considered Paleozoic, and members of the other family, Kennedyidae, are closer to Early Permian than to Triassic forms. Elements conditionally considered Paleozoic also prevail among Coleoptera, Neuroptera, and Corydalida. Among Coleoptera, the families Permocupedidae and Rhombocoleidae are considered as Paleozoic and the family Taldycupedidae, as post-Paleozoic. Neuroptera and Corydalida are represented by families considered Paleozoic: Permithonidae and Parasialidae, respectively. Among Hemiptera and Panorpida, the numbers of families considered Paleozoic and post-Paleozoic are equal. Among Hemiptera, the families considered Paleozoic are Prosbolidae, Ingruidae, and Pereboreidae, and the families considered post-Paleozoic are Stenoviciidae, Dunstaniidae, and Progonocimicidae; among Panorpida, Robinjohniidae and Mesopsychidae, respectively. Among Trichoptera, only one family has been found, Cladochoristidae; it is considered Paleozoic. The orders Machilida, Thripida, Psocida, and Jurinida are represented by transitional families. Among members of the infraorder Scarabaeones found in Isady, elements considered post-Paleozoic are rather common, although they usually play a minor part, having a subordinate position within their groups. The only exceptions are Mesopsychidae, subdominant among Panorpida (this family includes one of two most abundant scorpionfly species in Isady, *Permopsyche issadensis*), and, possibly, Cladochoristidae (Trichoptera); however, the extremely insufficient number of caddisflies in the collection allows only preliminary conclusions.

The infraclass Gryllones is represented by 11 families considered Paleozoic and seven considered post-Paleozoic. The order Eoblattida, which proved surprisingly diverse for the Late Permian, is entirely Paleozoic. Eoblattids are represented by two families, Idelinellidae known from the Upper Carboniferous to Upper Permian (Aristov and Rasnitsyn, 2012) and Soyanopteridae known from the Lower to Upper Permian (Aristov and Rasnitsyn, 2011). In addition, there is a fragment of a very large wing of endemic *Issadische maximum* Aristov, 2013 (Aristov, 2013b*)*, which cannot be attributed with certainty to any family of Eoblattida. The Grylloblattida fauna of Isady has a Paleozoic pattern because of the taxonomic and numerical (about 14% of specimens identifiable to family) dominance of families that do not cross the Permian–Triassic boundary (Cacurgidae, Kortshakiliidae, Permulidae, Permotermopsidae, and Liomopteridae, represented by a total of seven genera and seven species). The earliest of these families is Cacurgidae, known from the Upper Carboniferous and Lower Permian. The abundance of the families considered Paleozoic is higher than that of families considered post-Paleozoic. The latter category is represented by Mesortopteridae and Tunguskapteridae, which make up about 2% of specimens and include one genus and one species each. The largest (84%) and most diverse part of Grylloblattida is represented by transitional families (appearing earlier than the Urzhumian and becoming extinct later than the Induan): Chauliodítidae, Megakhosaridae, Geinitziidae, and Blattogryllidae. Endemic families are absent.

The Paleozoic pattern is less characteristic of the Perlida fauna (three families are considered as Paleozoic and two, as post-Paleozoic). As among Grylloblattida, elements considered Paleozoic dominate taxonomically and numerically. The most diverse and abundant family is Palaeonemouridae, which is considered Paleozoic; Paleoperlidae and Tshekardoperlidae, considered Paleozoic, and Euxenoperlidae and Eusteniidae, considered post-Paleozoic, are infrequent or sporadic. The recent stonefly family Eustheniidae is conditionally considered post-Paleozoic, with some reservation, because this family has been recorded in the Late Permian and has not in the Mesozoic.

Among Orthoptera, there is one family considered Paleozoic and one considered post-Paleozoic (Pruvostitidae and Proparagryllacrididae, respectively). The order Blattida looks least Paleozoic due to two families considered post-Paleozoic (“Argentinoblattidae” and Caloblattinidae) and the absence of presumably Paleozoic families. The orders Dermaptera, Phasmatida, and Mesotitanida are represented by elements considered to be endemic. In general, members of the infraclass Gryllones have a more Mesozoic pattern than members of the infraclass Scarabaeones primarily due to Orthoptera and Blattida. In addition, the only endemic family, Alexarasniidae Gorochov, 2011, represented by *Alexarasnia rossica* Gorochov, 2011, was described in Polyneoptera (= Gryllones). This family has not been assigned in the original description to any particular order of Polyneoptera (Gorochov, 2011).

The systematic list of insects found in the Isady locality is given below. Genera and species that have been recognized as new but have not yet been given a scientific name are excluded from the list. For taxa of family rank and higher, ↑ designates the first appearance, ↓ means the last appearance, and ↕ means endemics.

Machilida Grassi, 1888 (=Archaeognatha Burner, 1904)
- Dasyleptidae Sharov 1957 (Fig. 6b)

Ephemerida Latreille, 1810 (=Ephemeroptera Hyatt et Arms, 1890, sensu lato)
- ↓Protereismatidae Sellards, 1907
  - *Alexandrinia gigantea* Sinitshenkova et Vassilenko, 2012
  - *Ponalex maximus* Sinitshenkova et Aristov, 2012
- Misthodotidae Tillyard, 1932
  - *Misthodotes tshernovae* Sinitshenkova et Vassilenko, 2012 (Sinitshenkova and Aristov, 2012; Sinitshenkova and Vassilenko, 2012)

Odonata Fabricius, 1792
- Permolestidae Martynov 1932
- Kennedyidae Tillyard 1925

↓Caloneurida Handlirsch, 1906
- ↓Caloneuridae Handlirsch, 1906
  - *Issadistica issada* Rasnitsyn et Aristov, gen. et sp. nov.
  - *I. longa* Rasnitsyn et Aristov, gen. et sp. nov.
  - *Euthygramma* Martynov 1928

Hypoperlida Martynov, 1928
- ↓Hypoperlina Martynov, 1928
  - ↓Hypoperlidae Martynov, 1928
  - *Idelopsocus mutovinus* Rasnitsyn et Aristov, sp. nov.
  - Strephocladina Martynov 1938
- Ischnoneuridae Handlirsch, 1906
  - *Strephoptilus borealis* Rasnitsyn et Aristov, gen. et sp. nov.
  - *S. longus* Rasnitsyn et Aristov, gen. et sp. nov.

↓ Dictyoneurida Handlirsch, 1906 (=Palaeodictyoptera Goldenberg, 1854)
- ↓Calvertiellidae Martynov, 1931 (Fig. 6a)

↓Mischopterida Handlirsch, 1906 (=Megasecoptera Brongniart, 1893 + Archodonata Martynov, 1932)
- ↓Moravohymenidae Kukalová-Peck 1972
  - *Issadohymen ponomarenkoi* Sinitshenkova et Aristov, gen. et sp. nov.

Psocida Leach, 1815 (=Psocoptera Shipley, 1904)
- Psocidiidae Tillyard, 1926

Thripida Fallen, 1914 (=Thysanoptera Haliday, 1836)
- Lophioneuridae Tillyard, 1921 (Fig. 6f)

Hemiptera Linné, 1758
- Sternorrhyncha Meyers et China 1929
  - Protopsyllidiidae Carpenter, 1931 (Fig. 6d)
- Auchenorrhyncha Duméril, 1806
  - Ingruidae Becker-Migdisova, 1960
  - Scytinopteridae Handlirsch, 1906
  - Stenoviciidae Evans, 1956
  - Pereboriidae M. Zalessky, 1930
  - Dunstaniidae Tillyard, 1916
  - Prosbolidae Handlirsch, 1906
  - Dysmorphoptilidae Handlirsch, 1906
  - ↑Coleorrhyncha Myers et China 1929
  - ↑Progonocimicidae Handlirsch, 1906 (Fig. 6e)

Palaeomanteida Handlirsch, 1906 (=Miomoptera Martynov, 1927)
- Permosialidae Martynov, 1928
  - *Epimastax mutovinensis* Aristov et Rasnitsyn, sp. nov.
- ↓Palaeomanteidae Handlirsch, 1906
  - ?*Tridelopterum indebitum* Rasnitsyn et Aristov, sp. nov.
- ↓Permembiidae
  - *Issapaloptera infracta* Rasnitsyn et Aristov, gen. et sp. nov.
  - *Neembia ampla* Rasnitsyn et Aristov, gen. et sp. nov.

Coleoptera Linné, 1758
- Permocupedidae Martynov, 1933
  - *Protocupoides esini* Ponomarenko, sp. nov.
- Taldycupedidae Rohdendorf, 1961
  - *Taldycupes cellulosus* Ponomarenko, sp. nov.
  - *Simmondsia permiana* Ponomarenko, sp. nov.
- Asiocoleidae Rohdendorf, 1961
  - *Bicoleus laticella* Ponomarenko, sp. nov.
  - *Tetracoleus tricoleoides* Ponomarenko, sp. nov.
- Rhombocoleidae Rohdendorf, 1961
  - *Karakanocoleus mutovinensis* Ponomarenko, sp. nov.
  - *Erunakicupes grossus* Ponomarenko, sp. nov.
  - *Rossocoleus aristovi* Ponomarenko, sp. nov.
- Schizocoleidae Rohdendorf, 1961
  - *Schizocoleus depressus* Ponomarenko, sp. nov.
  - *Uskatocoleus micron* Ponomarenko, sp. nov.
  - *U. sukhonenis* Ponomarenko, sp. nov.
  - *U. convexus* Ponomarenko, sp. nov.
  - *Pseudochrysomelites bashkuevi* Ponomarenko, sp. nov.
  - *P. sphenoidalis* Ponomarenko, sp. nov.
  - *P. medialis* Ponomarenko, sp. nov.

    - *P. longus* Ponomarenko, sp. nov.

Corydalida Leach, 1815 (=Megaloptera Latreille, 1802)

- Parasialidae Ponomarenko, 1977

Neuroptera Linné, 1758 (Fig. 6g)

- Permithonidae Tillyard 1922 (Fig. 6h)
    - *Permithonopsis* Martynov 1932

Jurinida Zalessky, 1928 (=Glosselytrodea Martynov, 1938)

- Jurinidae Zalessky, 1929
    - *Issadelytron speciosum* Rasnitsyn et Aristov, gen. et sp. nov.
- Glosselytridae Martynov, 1938
    - ?*Karajurina desperata* Aristov et Rasnitsyn, sp. nov.

Panorpida Latreille, 1802 (=Mecoptera Packard, 1886)

- Permochoristidae Tillyard, 1917 (Fig. 6i)
- Agetopanorpinae Carpenter, 1930
    - *Agetopanorpa danili* Bashkuev, sp. nov.
- Pemochoristinae Tillyard, 1917
    - *Neudolbenus kopylovi* Bashkuev, gen. et sp. nov.
    - *N. giganteus* Bashkuev, gen. et sp. nov.
    - *Tatarakara variomaculata* Bashkuev, sp. nov.
    - *Mesochorista generalis* Bashkuev, sp. nov.
    - *Permeca pygmaea* Bashkuev, sp. nov.
    - *P. media* Bashkuev, sp. nov.
- ↑Mesopsychidae Tillyard, 1917
    - *Permopsyche issadensis* Bashkuev, 2011
    - *P. rasnitsyni* Bashkuev, 2011 (Bashkuev, 2011b)
- ↑Nedubroviidae Bashkuev, 2011 ↑
    - *Nedubrovia shcherbakovi* Bashkuev, 2011 (Bashkuev, 2011a)
- ↑Permotanyderidae Riek, 1953 (Fig. 6j)
- ?Robinjohniidae O. Martynova, 1948

Trichoptera Kirby, 1815

- Cladochoristidae Tillyard 1926
    - *Cladochorista issadica* Sukacheva et Aristov, sp. nov.

↓ Eoblattida Handlirsch, 1906

- ↓Idelinellidae Storozhenko, 1997
    - *Permeoblatta borealis* Rasnitsyn et Aristov, 2010 (Rasnitsyn and Aristov, 2010; Aristov, 2013b)
- ↓Soyanopteridae Aristov et Rasnitsyn, 2011
    - *Poldarsia relictaria* Aristov et Rasnitsyn, 2011 (Aristov and Rasnitsyn, 2011)
- Eoblattida incertae familia
    - *Issadische maximum* Aristov, 2013 (Aristov, 2013b*)*

Blattida Latreille, 1810

- ↑Mutoviidae Vršanský et Aristov, 2012
    - *Mutovia intercalaria* Vršanský et Aristov, 2012 (Vršanský and Aristov, 2012)
- Phylloblattidae Schneider, 1983
    - *Aissoblatta* Handlirsch, 1904
- Caloblattinidae Vršanský et Ansorge, 2000
    - *Caloblattina* Vršanský et Ansorge, 2000
- Argentinoblattidae Martins-Neto et Gallego, 2005
    - *Voltziablatta* Papier et Grauvogel-Stamm, 1995
- Subioblattidae Schneider, 1983

Grylloblattida Walker, 1914 (see Chapter 2.6)

- Chauliodititidae Handlirsch, 1906
    - *Chauliodites ponomarenkovi* Aristov, 2008 (Aristov, 2008a)
    - *C. issadensis* Aristov, 2009 (Aristov, 2009c)
    - *C. circumornatus* Aristov, sp. nov.
    - *C. geniatus* Aristov, sp. nov.
    - *Parachauliodites orthopteroides* Aristov, 2013 (Aristov, 2013a)
    - *Purtovinia ustyugensis* Aristov, gen. et sp. nov.
    - *Permyak involucris* Aristov, gen. et sp. nov.
- Geinitziidae Handlirsch, 1906
    - *Geinitzia subita* Aristov, sp. nov.
    - *Shurabia permiana* Aristov, sp. nov.
    - *Sukhonia coriacea* Aristov, gen. et sp. nov.
- ↓Cacurgidae Handlirsch, 1906
    - *Kitchuga ryzhkovae* Aristov, 2012 (Aristov, 2012)
- Liomopteridae Sellards, 1909
    - *Liomopterites suhonensis* Aristov, 2009 (Aristov, 2009c)
    - *Sylvaella semicolorata* Aristov, sp. nov.
    - *Liomofrater circumcisus* Aristov, gen. et sp. nov.
    - *Falseshurabia transitoria* Aristov gen. et sp. nov.
- ↑Mesorthopteridae Tillyard, 1916
    - *Mesoidelia gorochovi* Aristov, sp. nov.
- ↓Permotermopsidae Martynov, 1937
    - *Permofossilis commasticatus* Aristov, 2013 (Aristov, 2013a)
- Megakhosaridae Sharov, 1961
    - *Parakhosara kopylovi* Aristov, 2009 (Aristov, 2009c)
    - *P. mutoviensis* Aristov, 2009 (Aristov, 2009c)
    - *P. reticulata* Aristov, sp. nov.
    - *Megakhosarodes tensilis* Aristov, 2013 (Aristov, 2013a)
- *Abbrevikhosara ovoidea* Aristov, gen. et sp. nov.
- Blattogryllidae Rasnitsyn, 1976
    - *Baharellinus dilaceratus* Aristov, 2013 (Aristov, 2013a)
    - *B. porrectus* Aristov, sp. nov.
- Tunguskapteridae Storozhenko et Vršanský, 1995
    - *Issadoptera bipectinata* (Aristov, 2009) (Aristov, 2009c)
- ↓Kortshakoliidae Storozhenko, 1997
    - *Vologdoptera maculosa* Aristov, 2009 (Aristov, 2009c)
- ↓Permulidae Aristov et Storozhenko, 2011
    - *Mezenalicula conjuncta* Aristov et Storozhenko, 2011 (Aristov and Storozhenko, 2011)
- Grylloblattida incertae sedis
    - *Sukhonoptera insolita* Aristov, 2009 (Aristov, 2009c)
    - *Issadonympha oculea* Aristov, gen. et sp. nov.

Kenguronympha lenta Aristov, gen. et sp. nov.
Perlida Latreille, 1810 (=Plecoptera Burmeister, 1839) (see Chapter 2.7)
Perlina Latreille, 1802
Gripopterygomorpha Enderlein, 1909
↑Eusteniidae Tillyard, 1921
Boreoperlidium borealis Sinitshenkova, gen. et sp. nov.
↑Euxenoperlidae Enderlein, 1909
?Gondwanoperlidium Pinto et Purper, 1978
Perlomorpha Latreille, 1802
Palaeoperlidae Sharov, 1961
Properla issadensis Sinitshenkova, sp. nov.
Kargaloperla decipiens Sinitshenkova, sp. nov.
K. furcata Sinitshenkova, sp. nov.
↓Tshekardoperlidae Sinitshenkova, 1987
Issadoperla permiana Sinitshenkova, gen. et sp. nov.
Perlomorpha incertae familia
Mirumoperla multinerva Sinitshenkova, gen. et sp. nov.
Nemourina Newman, 1853
Palaeonemouridae Sharov, 1961
Palaeonemoura issadensis Sinitshenkova et Aristov, 2010 (Sinitshenkova and Aristov, 2010)
P. amica Sinitshenkova, sp. nov.
P. antrorsa Sinitshenkova, sp. nov.
Palaeotaeniopterix laeta Sinitshenkova et Aristov, 2010
P. triternata Sinitshenkova et Aristov, 2010 (Sinitshenkova and Aristov, 2010)
P. dejecta Sinitshenkova, sp. nov.
P. constricta Sinitshenkova, sp. nov.
P. adjecta Sinitshenkova, sp. nov.
P. succida Sinitshenkova, sp. nov.
P. amissa Sinitshenkova, sp. nov.
P. fixa Sinitshenkova, sp. nov.
P. mira Sinitshenkova, sp. nov.
Palaeonemourisca diluta Sinitshenkova, sp. nov.
P. formalis Sinitshenkova, sp. nov.
Vottaknemoura admiranda Sinitshenkova, gen. et sp. nov.
Forficulida Latreille, 1810 (=Dermaptera DeGeer, 1773 + Protelytroptera Tillyard, 1931)
Dermelytridae Kukalová, 1966
Orthoptera Olivier, 1789
Ensifera Chopard, 1920
Elcanidea Handlirsch, 1906
Permelcanidae Sharov, 1962
Meselcaninae Gorochov, 1989
Meselcana vologodica Gorochov, sp. nov.
Oedischiidea Handlirsch, 1906
Pruvostitidae M. Zalessky, 1929
Suchonoedischia incompleta Gorochov, gen. et sp. nov.
↑Proparagryllacrididae Riek, 1956
Archifergania issadyensis Gorochov, gen. et sp. nov.
?Mesotitanida Tillyard, 1925 (=Titanoptera Sharov, 1968)
Deinotitanidae Gorochov, 2007, stat. nov.
Monstrotitan monstrosus Gorochov, gen. et sp. nov.
Phasmatida Leach, 1915
Superfamilia Prochresmodoidea Vishniakova, 1980
↓?Permophasmatidae Gorochov, 1992
Issadyphasma bashkuevi Gorochov, gen. et sp. nov.
I. suchonae Gorochov, sp. nov.
I. deminutum Gorochov, sp. nov.
Gryllones ordinis incertis
↕ Alexarasniidae Gorochov, 2011
Alexarasnia rossica Gorochov, 2011 (Gorochov, 2011)

1.2.4. Review of Plants

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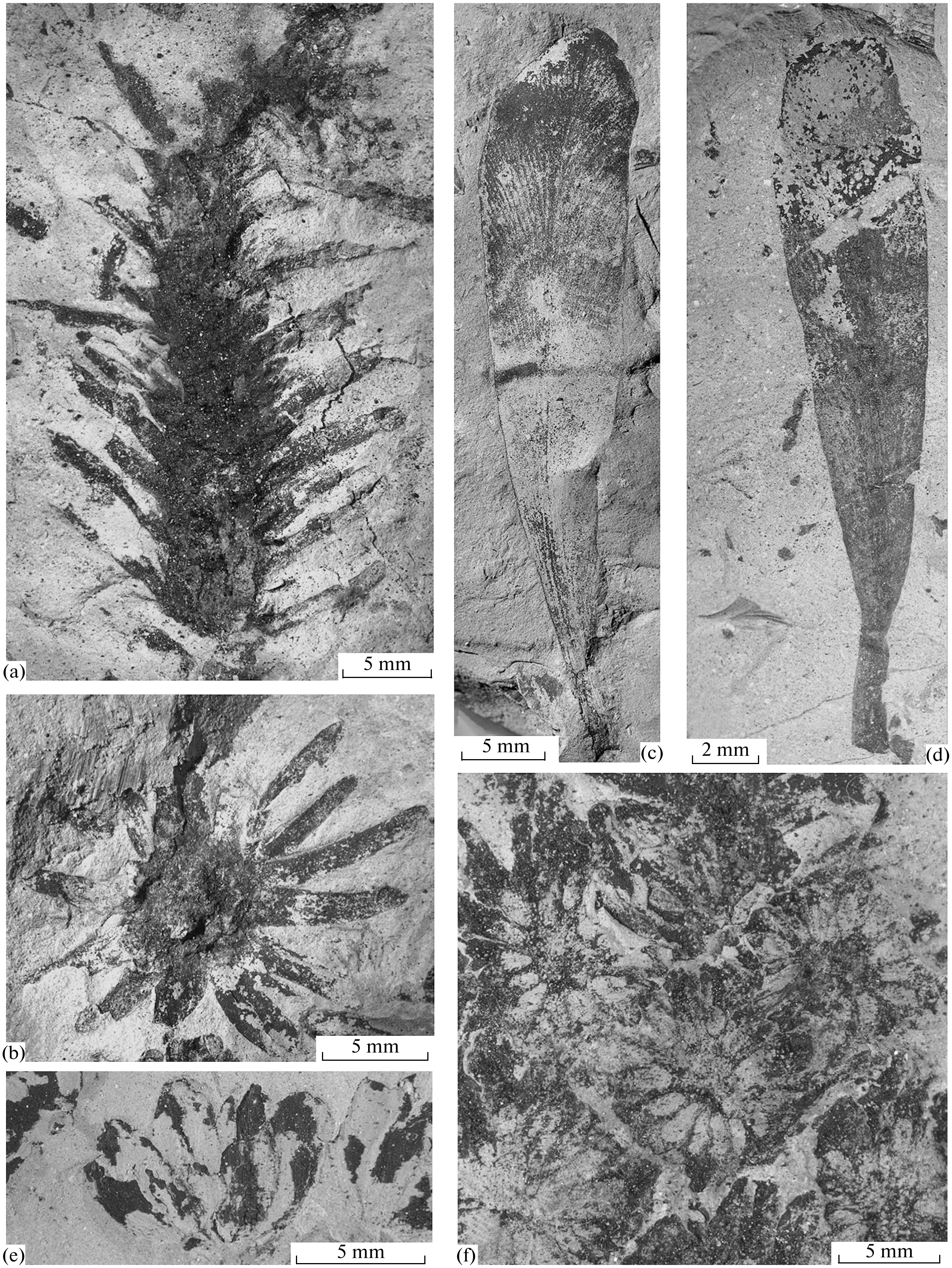
Fossil plants of the Isady locality are described in monographs of S.V. Meyen and A.V. Gomankov and belong to typical representatives of the *Tatarina* flora (Gomankov and Meyen, 1986; Meyen, 1997). The dominant fossils among them are shoots of the conifer *Quadrocladus schweitzeri* Meyen, 1986 (Figs. 7a, 7b) in association with strobiles of *Dvinostrobus sagittalis* Gomankov et Meyen, 1986. The subdominant fossils are leaves of the peltasperm pteridosperm *Tatarina conspicua* Gomankov et Meyen, 1979 (Figs. 7c, 7d) in association with peltate ovuliphores of *Peltaspermopsis* cf. *buevichae* Gomankov et Meyen, 1986 (Fig. 7e), seeds of *Salpingocarpus bicornutus* Meyen, 1986 and *S. variabilis* Meyen, 1986 and sporangia of *Permotheca striatifera* Meyen et Gomankov, 1986 (Fig. 7f), and *P. vesicasporoides* Meyen, Esaulova et Gomankov, 1986. Leaves of the cardiolepids *Phylladoderma* (subgenus *Aequistomia*) *annulata* Meyen, 1986, *P.* (*A.*) *rastorguevii* Meyen, 1986, and *P.* (*A.*) *trichophora* Meyen, 1986 are also abundant. Spore-bearing plants are represented by leaves and megaspores of the lycapod *Lepidophylloides delicata* (Gomankov) Gomankov, 2002. Other fossil plants found in the Isady locality include leaves with venation of the *Taeniopteris* type, referred by Gomankov (Gomankov and Meyen, 1986) to a separate fern genus, *Fefilopteris* Gomankov, 1986.


(a)
5 mm
(b)
5 mm
5 mm
(c)
2 mm
(d)
(e)
5 mm
(f)
5 mm

Gomankov and Meyen (1986) also reported on the finds of leaves of the *Rhaphidopteris* type and leaf fragments of uncertain systematic position referred to as *Arisada densa* Meyen, 1986.

New records of fossil plants include an interesting impression of a complex polysperm. This is a leaved shoot fragment followed by the fertile zone. Leaves on the leaved part of the shoot are arranged spirally and similar in morphology to leaves of *Quadrocladus schweitzeri* Gomankov et Meyen. The shoot axis is straight, 3–4 mm thick. The fertile zone is about 35 mm long and about 15 mm wide; it consists of the axis and spirally arranged axillary complexes (Figs. 8a, 8b). The bracts are free, lanceolate (Fig. 8c), 10 mm long and 3 mm wide. The abaxial surface of the bract bears a central carina (Fig. 8d), which can be traced to the point where the bract is attached to the shoot axis (Fig. 8e). Seed scales are more or less bilaterally symmetrical, 5 mm wide and 4 mm long; the distal part of the seed scale is divided by narrow sinuses into at least nine lobes; the apices of the lobes are rounded. The basal part of the seed scale smoothly narrows into a thin peduncle 3 mm long (Fig. 8f). On five lobes, oval contours are visible, interpreted as seed scars (Fig. 8g). Judging from the number of the oval contours, the number of ovules was probably at least five per seed scale. Figure 8c shows the abaxial surface of the bract, followed by a seed scale fragment without oval contours, which suggests that ovules were attached to the adaxial surface of the sporophyll. One complete ovule and several ovule fragments have been found, oriented parallel to the base of the seed scale. After maceration, several stuck pollen grains of the *Protohaploxipinus* type were found on the seeds. Associated vegetative shoots are of the *Geinitzia* sp. type. The position of the strobilus described in the system of Paleozoic conifers is not fully clear. The new specimen should probably be assigned to the voltzian conifer group in the sense proposed by Meyen (1997).

Gomankov (2002) assigned the flora of the Isady locality to the Aleksandrovka Paleofloristic Assemblage, indicating the almost total disappearance of Cordaitales and absence of sphenophytes of the genus *Sphenophyllum* as its differences from the preceding Kotel'nich Assemblage and the lower diversity of peltasperms as its difference from the succeeding Vokhma Assemblage. According to palynological data, the stratigraphic range of the Aleksandrovka Assemblage is limited to the Kovrov beds of the Severodvinian Stage. Note that the composition of the macroflora of Isady has a strong similarity with that of the Aristovo locality (Vologda Region). The flora of Isady, compared to Aristovo, is less rich at the species level; it was only in these two localities that the plants *Fefilopteris pilosa* and *Arisada densa,* specific for the *Tatarina* flora, have been found.

1.3. Vyatkian–Olenekian Localities

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Vyatkian fossil insects from European Russia are known from the Aristovo locality in the Vologda Region and from several localities in the Vladimir Region.

Aristovo. Vologda Region, Velikoustyugskii District, right bank of the Lesser Northern Dvina River near the village of Aristovo. The deposits belong to the Komaritsa Member, Salarevo Formation, Upper Vyatkian Substage, Vyatkian Stage (Arefiev et al., 2011), and to the *Chroniosuchus paradoxus* Subzone of the *Scutosaurus karpinskii* Tetrapod Zone (Golubev, 2000). The material comes from deposits of an oxbow lake. Specimens found in argillites include plant remains, conchostracans, ostracodes, chelicerates, and insects collected by S.V. Meyen (in 1972) and by expeditions of the Arthropoda Laboratory, PIN (in 2005 and 2011).

The collection of about 250 specimens stored in PIN consists mostly of Blattida, which compose about 90% of specimens. In addition to Blattida, rather infrequent Hemiptera, Coleoptera, Panorpida, Grylloblattida, and Perlida have been found in the locality.

Hemiptera Linné, 1758

- Stenoviciidae Evans, 1956
- Dunstaniidae Tillyard, 1916 (D.E. Shcherbakov, pers. comm., 2011)

Coleoptera Linné, 1758

- Asiocoleidae Rohdendorf, 1961
  - *Tetracoleus permianus* Ponomarenko, sp. nov.
- Schizocoleidae Rohdendorf, 1961
- Permosynidae Tillyard, 1924

Panorpida Latreille, 1802

- Permochoristidae Tillyard, 1917
  - *Mesochorista* Tillyard, 1916
  - *Tatarakara* Novokshonov, 1995
  - *Petromantis* Handlirsch, 1904
- Permotanyderidae Riek, 1953 (A.S. Bashkuev, pers. comm., 2011)

Fig. 7. Plants of the Isady locality, Vologda Region; Severodvinian Stage: (a, b) shoot of the conifer *Quadrocladus schweitzeri* Meyen, 1986: (a) specimen PIN, no. 5339/10, habitus, (b) specimen PIN, no. 5339/9, transverse split; (c, d) *Tatarina conspicua* Gomankov et Meyen, 1979, impressions of leaves: (c) specimen PIN, no. 5339/170; (d) specimen PIN, no. 5339/171; (e) assemblage of seed-bearing disks of *Peltaspermopsis* cf. *buevichae* Gomankov et Meyen, 1986, specimen PIN, no. 5339/6; (f) impression of sporangia of *Permotheca striatifera* Meyen et Gomankov, 1986, specimen PIN, no. 5339/3.

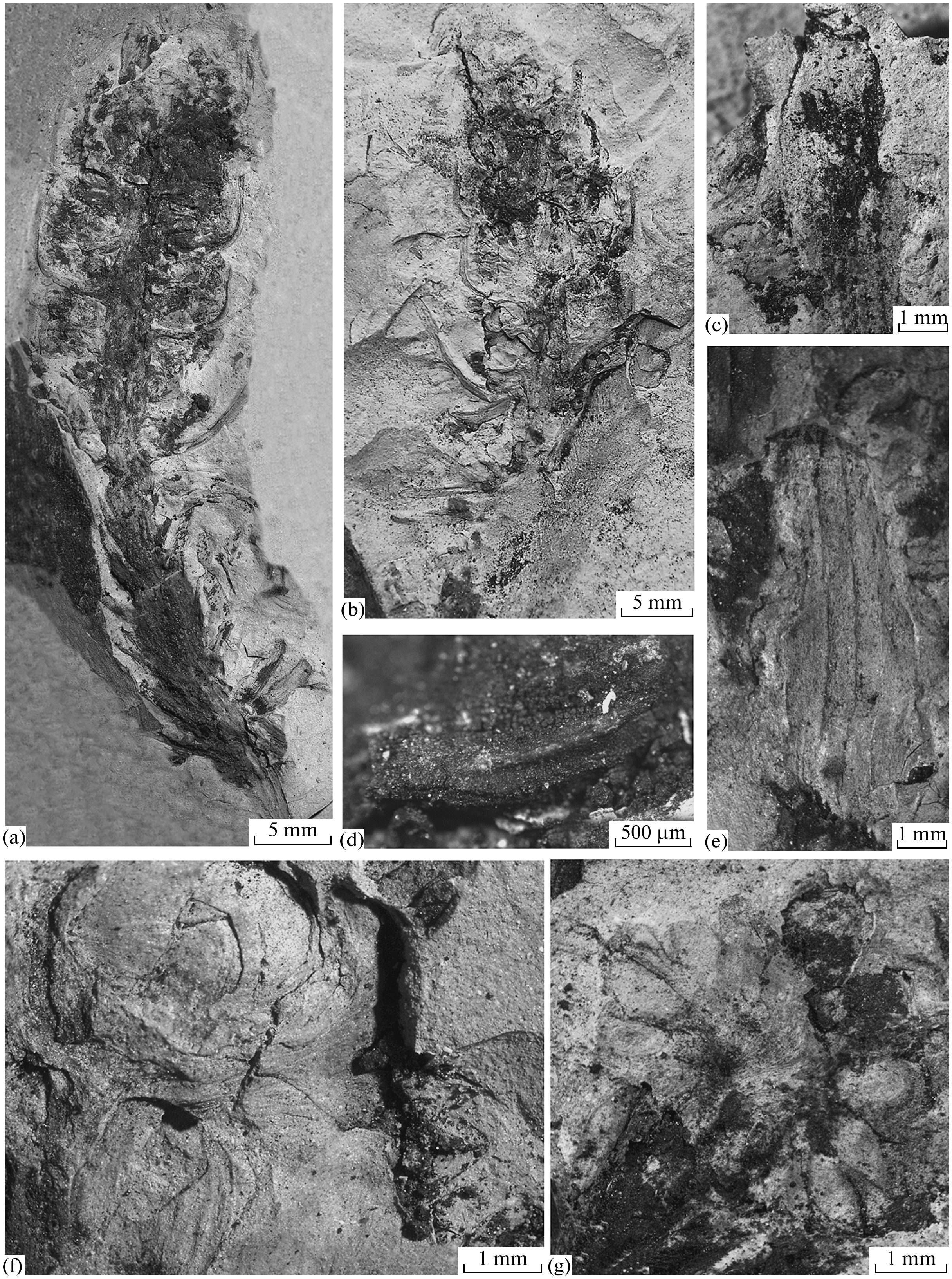

Fig. 8. Racemose megastrobilus of a voltzian conifer, specimen PIN, no. 5339/151, Isady locality, Vologda Region; Severodvinian Stage: (a) habitus of megastrobilus; (b) the same, counter impression; (c) impression of bract, adaxial view; (d) impression of bract, abaxial view; (e) base of bract, lateral view; (f) impression of adaxial surface of seed scale; (g) impression of seed scale with lobes.

Blattida Latreille, 1810
- Phylloblattidae Schneider, 1983
  - *Aissoblatta* Handlirsch, 1904
- Mutoviidae Vršanský et Aristov, 2012.

Grylloblattida Walker, 1914
- Chauliodititidae Handlirsch, 1906
  - *Chauliodites antiquus* (Aristov, 2003) (Aristov, 2003)
  - *Dvinopedes salariovensis* Aristov, 2013 (Aristov, 2013a)
- Liomopteridae Sellards, 1909
  - *Expartolioma hirta* Aristov, 2004 (Aristov, 2004e)
- Megakhosaridae Sharov, 1961 (Aristov, 2008b)

Perlida Latreille, 1810
- Palaeonemouridae Sharov, 1961 (N.D. Sinitshenkova, pers. comm., 2011)

Because of the unique stratigraphic position of localities in the town of **Vyazniki** and its environs (Vladimir Region, Vyaznikovskii District), they are discussed here in more detail. Three fossil insect localities are known in this area, which are outcrops of contemporaneous argillites of lacustrine origin (A.G. Sennikov, pers. comm., 2011). The Vyazniki deposits belong to the Gorokhovets Member of the Obnora Formation, *Archosaurus rossicus* Tetrapod Zone and *Gnathorhiza otschevi–Mutovinia sennikovi* Ichthyozone of the Upper Vyatkian Substage, Vyatkian Stage, Upper Permian. These deposits have been recognized as the Vyaznikian Horizon (Shishkin, 1990) or Vyaznikovian Stage (Lozovskii and Kukhtinov, 2007). It has recently been suggested to refer deposits found in the environs of the towns of Vyazniki and Gorokhovets to the Zhukovian Horizon, the latest Permian horizon, immediately underlying Lower Triassic deposits (Sennikov and Golubev, 2010). The Zhukovian Horizon includes the Balymotikha, Sokovka, and Mys Bykovka localities. Although these deposits are presumably contemporaneous, they display a number of differences, making it necessary to describe them separately. The entomofaunas of these localities have been characterized unevenly.

Mys Bykovka. Vyaznikovskii District, the uppermost part of the right slope of the Klyazma River valley at the western outskirts of the village of Bykovka, immediately upstream from the mouth of the Bykovskii gully. Coordinates (the data used hereinafter are Pulkovo 1942) are 56.258336° N, 42.087499° E. The locality has yielded only one insect specimen of the cockroach *Aissoblatta* sp. (Phylloblattidae), found by the expedition of the Arthropoda Laboratory, PIN, in 2010 and stored in PIN.

Sokovka. Right bank of the Klyazma River, short deep gully at the northeastern outskirts of the town of Vyazniki, 56.256346° N and 42.105239° E. Fossils found in gray thin-layer clays include plant remains, conchostracans, abundant ostracodes, chelicerates, and rather infrequent insects. Plants are represented by large, well-preserved fragments. Because of this, plants and traces of interactions between plants and arthropods are known among the localities of the Vyazniki area mostly from Sokovka. The dominant plant fossils are peltasperms, which make up about 50% of specimens. Leaves of *Vjaznikopteris rigida* Naugolnykh, *Permophyllocladus polymorphus* Karasev et Krassilov, *Tatarina meyenii* (Naugolnykh) Karasev, and *T. conspicua* Meyen and seed-bearing discs of *Peltaspermum capitatum* Naugolnykh are well represented. Ferns of the genera *Prynadaeopteris, Pecopteris,* and sphenophytes *Neocalamites* cf. *mansfeldicus* (Weigelt) Weigelt are rarer. Seed-bearing organs of *Stiphorus ovatum* Naugolnykh and leaves of *Doliostomia* (or *Sphenobaiera*) sp., assigned to ginkgophytes, have been found. Conifers are represented by leaf fragments of *Pseudovoltzia liebeana* (Geinitz) Florin and a few female and male strobiles (Naugolnykh, 2006; E.V. Karasev, pers. comm., 2011). The flora of the Sokovka locality was treated in detail by Newell et al. (2010). The insects collected in Sokovka are not numerous. They have been collected by an expedition of the Arthropoda Laboratory, PIN, in 2004, and by expeditions of the Arthropoda Laboratory and Paleobotany laboratory, PIN, in 2004–2010.

A total of 17 insect specimens stored in PIN have been collected in Sokovka. They include members of Ephemerida, Thripida, Hemiptera, Coleoptera, Panorpida, Blattida, and Grylloblattida. The dominant order is Grylloblattida, eight specimens; Coleoptera, Blattida, Panorpida, and Thripida (Lophioneuridae) are less abundant (two specimens each); Hemiptera are represented by one specimen.

Thripida Fallen, 1914
- Lophioneuridae Tillyard, 1921

Coleoptera Linné, 1758
- Asiocoleidae Rohdendorf, 1961
  - *Tetracoleus sennikovi* Ponomarenko, 2011
- Permosynidae Tillyard, 1924
  - *Hydrobiites tillyardi* Ponomarenko, 2011 (elytron fragment; the same species is known also from the Balymotikha locality: Ponomarenko, 2011)

Panorpida Latreille, 1802
- Nedubroviidae Bashkuev, 2011
  - *Nedubrovia deformis* Bashkuev, 2011 (Bashkuev, 2011a)
- Permochoristidae Tillyard, 1917
  - *Tatarakara* Novokshonov, 1995 (A.S. Bashkuev, pers. comm., 2011)

Blattida Latreille, 1810
- "Argentinoblattidae" Martins-Neto et Gallego, 2005
  - *Voltziablatta* Papier et Grauvogel-Stamm, 1995 (P. Vršanský, pers. comm., 2011)

Grylloblattida Walker, 1914
- Chauliodititidae Handlirsch, 1906

Chauliodites afonini Aristov, 2008 (Aristov, 2008a)

Klyazmia karasevi Aristov, 2013 (Aristov, 2013a)

Balymotikha. Southern outskirts of the town of Vyazniki, left slope of the gully before its crossing with the highway east of the village of Balymotikha, 56.220203° N, 42.156813° E. Fossils found in this locality include plant remains, conchostracans, insects, fish scales, and tetrapod bones. In contrast to Sokovka, plant remains are rare here, and usually represented by rather small fragments; conchostracans are more abundant here than in Sokovka, ostracodes are rare, and insects are significantly more abundant. Fossil plants of Balymotikha have been studied less thoroughly than in Sokovka. The material studied shows that Balymotikha differs from Sokovka in the greater proportions of the fern *Prynadaeopteris* sp. (almost absent in Sokovka) and peltasperms (up to 80%). Peltasperms are represented by *Tatarina* cf. *conspicua, Tatarina* sp., *Permophyllocladus polymorphus* Karasev et Krassilov, *Phylladoderma* (*Aequistomia*) *aequalis* Meyen; leaves of *Vjaznikopteris* Naugolnykh, which are abundant in Sokovka, are absent in Balymotikha. Judging from the dispersed cuticles, the abundance of *Tatarina* in Balymotikha is higher. Conifers and ginkgophytes are absent (Naugolnykh, 2006; E.V. Karasev, pers. comm., 2011). The nature of these differences is possibly facies-related rather than age-related. The deposits of Sokovka were formed at some distance from the bank, under relatively constant conditions of an eutrophic lake or former riverbed. By contrast, the deposits of Balymotikha were formed under stronger hydrodynamics, as evidenced by the fact that plant remains are sorted and oriented by their longer axes in the same direction (Naugolnykh, 2006). Insects were collected by expeditions of the Arthropoda Laboratory, PIN, from 2005 to 2010.

The insect collection includes about 330 specimens stored in PIN. The dominant order is Blattida, 60% of all insect specimens (196 specimens); the subdominant order is Hemiptera 20% (64 specimens). Less abundant orders include Grylloblattida 6% (19 specimens), Coleoptera (5%; 15 specimens), Panorpida (4%; 13 specimens), and Trichoptera (2%; seven specimens). The orders Neuroptera and Orthoptera (three specimens each) make up 1% each; Perlida (two specimens), Thripida, Palaeomanteida, Forficulida, and Mesotitanida (one specimen each) make up less than 1% each.

Thripida Fallen, 1914
  Lophioneuridae Tillyard, 1921
Hemiptera Linné, 1758
  Protopsyllidiidae Carpenter, 1931
  Scitinopteridae Handlirsch, 1906
  Stenoviciidae Evans, 1956
  Pereboreidae M. Zalessky, 1930
  Dunstaniidae Tillyard, 1916
  Prosboleidae Handlirsch, 1906
  Dismorphoptilidae Handlirsch, 1906
  Surijokocixiidae Shcherbakov, 2000
  Paraknightiidae Evans, 1950
  Progonocimicidae Handlirsch, 1906
  (D.E. Shcherbakov, pers. comm., 2011)
Palaeomanteida Handlirsch, 1906
  Pemosialidae Martynov, 1928
    Balymotikha deterior Aristov et Rasnitsyn, gen. et sp. nov.
Coleoptera Linné, 1758
  Pemosynidae Tillyard, 1924
    Permosyne lata Ponomarenko, 2011
    P. tillyardi Ponomarenko, 2011
    Hydrobiites vladimiri Ponomarenko, 2011
  Schizocoleidae Rohdendorf, 1961
    Uskatocoleus rhynchophorus Ponomarenko, 2011
    U. eurypygus Ponomarenko, 2011
    Pseudochrysomelites major Ponomarenko, 2011
    Mertorhynchites baculum Ponomarenko, 2011
    M. elongatus Ponomarenko, 2011
  Rhombocoleidae Rohdendorf, 1961
    Erunakicupes angustus Ponomarenko, 2011 (Ponomarenko, 2011)
Neuroptera Linné, 1758
  Permithonidae Tillyard, 1922
  (A.G. Ponomarenko, pers. comm., 2011)
Panorpida Latreille, 1802
  Mesopsychidae Tillyard, 1917
    Mesopsyche incompleta Bashkuev, 2011 (Bashkuev, 2011b)
  Nedubroviidae Bashkuev, 2011
    Paranedubrovia novokshonovi Bashkuev, 2011
    P. minutissima Bashkuev, 2011 (Bashkuev, 2011a).
Trichoptera Kirby, 1815
  Microptysmatidae O. Martynova, 1958
    Kamopanorpa Martynov, 1928
  Cladochoristidae Riek, 1953
    Cladochoristella ryzhkovae Sukatsheva et Aristov, sp. nov.
  Prorhyacophilidae Riek, 1955
    Prorhyacophila rasnitsyni Sukatsheva et Aristov, sp. nov.
Blattida Latreille, 1810
  Phylloblattidae Schneider, 1983
    Aissoblatta Handlirsch, 1904
  Mutoviidae Vršanský et Aristov, 2012
    Mutovia Vršanský et Aristov, 2012
  “Argentinoblattidae” Martins-Neto et Gallego, 2005
    Voltziablatta Papier et Grauvogel-Stamm, 1995
  Mylacridae Scudder 1886 (P. Vršanský, pers. comm., 2011)
Grylloblattida Walker, 1914
  Megakhosaridae Sharov, 1961

Megakhosarina vyaznikensis Aristov, 2009 (Aristov, 2009b)

Megakhosarodes borealis Aristov, 2013 (Aristov, 2013a)

?Chauliodititidae Handlirsch, 1906

?Mesotitanida Tillyard, 1925

Deinotitanidae Gorochov, 2007, stat. nov.

Monstrotitan monstrosus Gorochov, gen. et sp. nov.

The list shows that of seven families, five genera, and four species of insects found in Sokovka the taxa shared with Balymotikha include five families: Lophioneuridae (Thripida), Pemosynidae (Coleoptera), Nedubroviidae (Panorpida), "Argentinoblattidae" (Blattida), and Chauliodititidae (Grylloblattida); two genera: *Voltziablatta* ("Argentinoblattidae") and *Permosyne* (Pemosynidae); and one species, *Permosyne vladimiri* Ponomarenko, 2011 (represented in Sokovka by an elytron fragment). Thus, the difference in the composition of insects is remarkable. In Balymotikha, where the sample size is much greater, the family Permochoristidae (Panorpida), the most common among Permian scorpionflies, is absent. The Sokovka entomofauna is dominated by Grylloblattida, while Blattida are only represented by two impressions. In Balymotikha, the situation is reverse: Blattida strongly dominate, while Grylloblattida are relatively infrequent. The situation with dominating Blattida and subordinate Grylloblattida is characteristic of the Upper Permian of European Russia. The situation with Grylloblattida more abundant or as abundant as Blattida is characteristic of the Lower Triassic (Aristov, 2004a; 2005b; Shcherbakov, 2008). However, the difference in faunal composition may be determined by differences in the distance from the bank and velocity of the current rather than by age-related differences (Naugolnykh, 2006). The relatively low similarity (for contemporaneous and geographically close insect faunas) in the composition and proportions of orders and the difference in the composition of other invertebrates and plants suggest that the faunas of Sokovka and Balymotikha should be considered separately.

The insect fauna of Balymotikha has a number of distinctive features, which make Balymotikha unique among Permian localities. The Panorpida fauna is characterized by the absence of Permochoristidae, the dominant family in most of the Permian deposits (Novokshonov, 1997). Another distinctive feature is the dominance of Blattida. This feature is not unique among Upper Permian localities of European Russia, where dominant Blattida are characteristic of most of the Severodvinian and Vyatkian localities. However, outside European Russia, Blattida are extremely infrequent or, more often, totally absent in Upper Permian localities. The dominant cockroach family in Balymotikha is "Argentinoblattidae." The situation with "Argentinoblattidae" dominating among Blattida is typical of the Voltzia sandstones of the Vosges (Anisian Stage of France). The family is known from the Upper Permian of Russia, dominating throughout the Triassic (described most thoroughly from the Vosges), and its latest representatives were described from the Upper Jurassic of Mongolia (Papier and Grauvogel-Stamm, 1995; Vishniakova 1998; Vršanský, 2008). The absence of the family Liomopteridae, which is observed in Balymotikha, is very unusual for the Permian. Liomopterids are the most common Permian grylloblattids, recorded in almost all Permian localities. They have been recorded in all Upper Permian localities, even in small collections and, outside European Russia, this family dominates among Grylloblattida (Aristov, 2009a). However, the largest Upper Permian locality of Grylloblattida in European Russia, Isady, demonstrates a rather low proportion of Liomopteridae (Aristov, 2009c; Chapter 2.6).

The age of the Nedubrovo Member of the Vokhma Formation is debatable. According to the resolution of the Interdepartmental Stratigraphic Committee of Russia from April 7, 2011, this formation is basal Triassic (Lozovskii et al., 2011). The entomofauna, which, along with the flora, is known mostly from the Nedubrovo locality (Vologda Region), was also dated Induan by Shcherbakov (2008). However, the flora is of the *Tatarina* type (typical of the terminal Permian) and belongs to the so-called "transitional interval." The term "transitional interval (beds) between the Permian and Triassic" was established in the literature to denote the chronostratigraphic interval (about 251.5 to 251 Ma) corresponding to the Upper Permian *Clarkina meishanensis–Hindeodus praeparvus* Conodont Zone (Korte, 2005; Karasev, 2009). The Vokhma Insect Assemblage (including the entomofauna of the somewhat later Entala and Sholga localities, Vologda Region) insignificantly differs in age-related features from assemblages of the Mal'tsevo Formation of the Kuznetsk Basin and intertrappean deposits of the Tunguska Basin, which are similar in carbon dating and also called transitional here (for more detail, see Chapter 3.1). In addition to the above-listed localities, rather infrequent Vokhma insects of European Russia are known from the Zalazna locality, Kirov Region.

Nedubrovo. Vologda Region, Kichgorodetskii District, left bank of the Kichmenga River near the village of Nedubrovo. The deposits belong to the Nedubrovo Member in the basal strata of the Vokhma Formation of the Vokhmian Horizon. The material comes from smectite clays with an admixture of ash matter deposited in an oxbow lake or shallow and rather large lake (Lozovskii et al., 2001). It includes plant remains, conchostracans, ostracodes, and scorpions (Fet et al., 2011), insects, and amphibians. The plant association is dominated by Zechstein elements, represented by leaves of *Quadrocladus solmsii* (Gothan et Nagathard) Schweitzer and *Ullmannia bronnii* Göppert and megaspores of *Otynisporites eotriassicus* Fuglewicz; considerable roles are played by *T. conspicua* Meyen, a Late Permian element of *Tatarina* flora, and by the transitional interval species *T. rinatata* Karasev. Other plant remains found in the Nedubrovo beds include rather infrequent ferns of the genera *Prynadaeopteris* Radczhenko and *Pecopteris* Brongniart (E.V. Karasev, pers. comm., 2011).

The material collected by expeditions of the Arthropoda Laboratory (in 1999, 2007, and 2011) and stored in PIN includes about 200 specimens. They represent the orders Psocida, Hemiptera, Palaeomanteida, Coleoptera, Panorpida, Blattida, Grylloblattida, and Orthoptera. The dominant orders are Hemiptera (25%) and Blattida (21%); Grylloblattida (17%), Panorpida, and Coleoptera (14% each) are less abundant. Psocoptera, Palaeomanteida, and Orthoptera are rather infrequent.

Psocida Leach, 1815
- Psocidiidae Tillyard, 1926

Hemiptera Linné, 1758
- Archescitinidae Tillyard, 1926
- Surijokocixiidae Shcherbakov, 2000
- Scytinipteridae Handlirsch, 1906 (Lozovskii et al., 2001)
- Progonocimicidae Handlirsch, 1906

Palaeomanteida Handlirsch, 1906
- Palaeomanteidae Handlirsch, 1906
  - *Delopterum* Sellards, 1909
- Permosialidae Martynov, 1928

Coleoptera Linné, 1758
- Schizocoleidae Rohdendorf, 1961
  - *Palademosyne latum* Ponomarenko, 2004 (Ponomarenko, 2004)
- Taldycupedidae Rohdendorf, 1961

Panorpida Latreille, 1802
- Nedubroviidae Bashkuev, 2011
  - *Nedubrovia mostovskii* (Novokshonov, Sukatsheva et Aristov, 2004) (Novokshonov et al., 2004; Bashkuev, 2011a)
- Permochoristidae Tillyard, 1917
  - Mesopsychidae Tillyard, 1917
- Permotanyderidae Riek, 1953 (A.S. Bashkuev, pers. comm., 2011)

Blattida Latreille, 1810
- Phylloblattidae Schneider, 1983 or primitive "Argentinoblattidae" Martins-Neto et Gallego, 2005
- "Argentinoblattidae" Martins-Neto et Gallego, 2005
  - *Voltziablatta* Papier et Grauvogel-Stamm, 1995 (P. Vršanský, pers. comm., 2011)

Grylloblattida Walker, 1914
- Chaulioditidae Handlirsch, 1906
  - *Chauliodites kitshmendensis* Aristov, 2013
  - *C. nedubrovensis* Aristov, 2013 (Aristov, 2013a)
- Blattogryllidae Rasnitsyn, 1976
  - *Protoblattogryllus nedubrovensis* Aristov, 2011 (Aristov, 2011a)

Orthoptera Olivier, 1789
- Permelcanidae Sharov, 1962
  - Meselcaninae Gorochov, 1989

Entala (=Yug, =Anan'ino). Vologda Region, Kichgorodetskii District, right bank of the Yug River 2 km downstream from the mouth of the Entala River. The deposits belong to the Sarafanikha or Anisimovo beds of the Vokhma Formation, Vokhmian Horizon (M.P. Arefiev, pers. comm., 2011). Fossils found in argillites of the oxbow lake include plant remains, conchostracans, insects, and tetrapods.

The material collected by M.P. Arefiev in 1993 and by an expedition of the Arthropoda Laboratory, PIN, in 1994 and stored in PIN includes about ten specimens. Insects are dominated by Coleoptera and individual Blattida and Grylloblattida.

Coleoptera Linné, 1758
- Schizophoridae Ponomarenko, 1968 (A.G. Ponomarenko, pers. comm., 2011)

Blattida Latreille, 1810
- Phylloblattidae Schneider, 1983
  - *Aissoblatta* Handlirsch, 1904 (P. Vršanský, pers. comm., 2011)

Grylloblattida Walker, 1914
- ?Chaulioditidae Handlirsch, 1906
  - *Yontala camura* Aristov, 2005 (Aristov, 2005a)

Sholga. Kirov Region, Podosinovskii District, left bank of the Yug River upstream from the village of Sholga, 200 m upstream from the ferry pier in the village of Sholga, 60°25′55.5″ N, 47°00′48.4″ E. Deposits of alluvial origin belong to the Ryabi or Astashikha beds of the Vokhma Formation, Vokhmian Horizon. In 2011, an expedition of the Arthropoda Laboratory found plant fragments, conchostracans, and a wing fragment tentatively assigned to Grylloblattida, which are stored in PIN.

Zalazna. Kirov Region, Omutninskii District, interfluve between the Belaya River and left tributaries of the Kama River (Tomyz' and Lytka rivers), 10–12 km southeast of the village of Zalazna, gully open into the Bol'shaya Zalazna Creek (tributary of the Belaya River) at its upper reaches. The deposits belong to the Vokhmian Horizon (Gomankov and Meyen, 1986). O.E. Chumakov found in 1965 seven insect specimens stored in PIN, three of which were identified, two Hemiptera and one Panorpida.

The only reliably Olenekian locality in European Russia and the only minimally representative reliably Olenekian locality in the world is **Tikhvinskoe** in the Yaroslavl Region (Rybinskii District, right bank of the Volga River near the village of Tikhvinskoe; Vetluga Group, Rybinskian Horizon, Rybinsk Formation, Parshino beds: Arefiev, 2007). Insects have been found in "bone-bearing breccias" and siltstones formed near the bank of a shallow water body of low salinity in a delta plain (Arefiev, 2007). According to another reconstruction, the water body ("Parshinskoe Lake") was brackish and connected in its western part with the open sea (Khodakovskaya et al., 2001). A total of

16 specimens have been collected, stored in PIN. Insects are represented in Tikhvinskoe by four orders: Coleoptera, Blattida, Grylloblattida, and Orthoptera. The insect assemblage is dominated by the orders Grylloblattida and Coleoptera. Grylloblattids are represented in Tikhvinskoe by a single species, *Chauliodites sennikovi* (Aristov, 2003) of the family Chaulioditidae (Aristov, 2003). Beetles are also represented by a single species, *Palademosyne elongatum* Ponomarenko, 2004 of the family Schizocoleidae (Ponomarenko, 2004). Beetle fossils are represented exclusively by smooth elytra, which probably belong to aquatic forms. Not a single elytron has been found that could have belonged to xylophagous beetles. Cockroaches are less abundant, represented by undescribed members of two families, Blattulidae and Caloblattinidae. The least abundant insect order in Tikhvinskoe is Orthoptera (Aristov et al., 2012).

1.4. Traces of Interactions between Arthropods and Plants from the Upper Permian Deposits of European Russia

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The deficiency of data on Permian traces of interactions between arthropods and plants is slowly disappearing, but truly complete and rich Late Permian assemblages of such traces remain infrequent. The richest and most complete of the assemblages described is that from the Upper Permian Normandien Formation (South Africa), in which almost all main types of interactions between insects and plants have been documented (Prevec et al., 2009).

The only rich assemblage of evidence of interactions between arthropods and plants known to date from the Upper Permian of European Russia is treated below, and new material from the Isady locality (=Mutovino lens = Mutovino) collected by expeditions of the Arthropoda Laboratory, PIN, in 2010 and 2011 is described.

Leaf galls. Distinctly pronounced structures on the leaf surface interpreted as insect galls are represented in the Isady locality by a new form and two previously described morphological types: (1) *Paleogallus shcherbakovi* Vasilenko, 2007, large, distinct, rounded structures on leaves, with linear or cruciform structures, which make the gall surface uneven, sometimes wavy with distinct ridges; (2) *Paleogallus gomankovi* Vasilenko, 2007, rounded structures, sometimes slightly elongate along veins, with a weak relief and even convex surface, and the perimeter bordered by a ring of concave relief (Vasilenko, 2007).

Family Paleogallidae Vjalov, 1975

Genus *Paleogallus* Vjalov, 1975

Paleogallus krassilovi Vassilenko, sp. nov.

Etymology. In honor of the paleobotanist V.A. Krassilov.

Holotype. PIN, no. 3840/2403, gall on a leaf of *?Tatarina* sp.; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 9a). Medium-sized symmetric fusiform swelling of leaf tissues, distinctly covered by surrounding tissues. The neoformation is oriented strictly along the long leaf axis, but has not pronounced confinement to any particular part of the leaf blade.

Measurements, mm. Gall length, 6; maximum width in central part, 1.1.

Comparison. The new species differs from all other species of the genus *Paleogallus* in the fusiform shape of the swelling of tissues and in the larger size.

Material. Holotype.

Traces of feeding on vegetative organs. Traces of feeding on leaf tissues are the most common type of fossil plant damage in the Isady locality. The prevalence of this type of damage is in general characteristic of the Permian (Beck et al., 1998, Labandeira, 1998, 2002; Beattie, 2005). Permian traces of leaf chewing and perforations are traditionally interpreted as feeding traces of insects of the orders Grylloblattida, Orthoptera, and Caloneurida (Labandeira, 1998). According to a different hypothesis, they could be produced by myriapods, which were abundant at that time and probably fed on fallen leaves (Ponomarenko, 1998).

Both marginal leaf damage, such as *Phagophytichnus rectus* Vasilenko, 2007 and *P. ekowskii* Amerom, 1966, and “window” perforations (*Folifenestra dubia* Vasilenko, 2007) are known from Isady. The *Phagophytichnus*-type damage is prevailing.

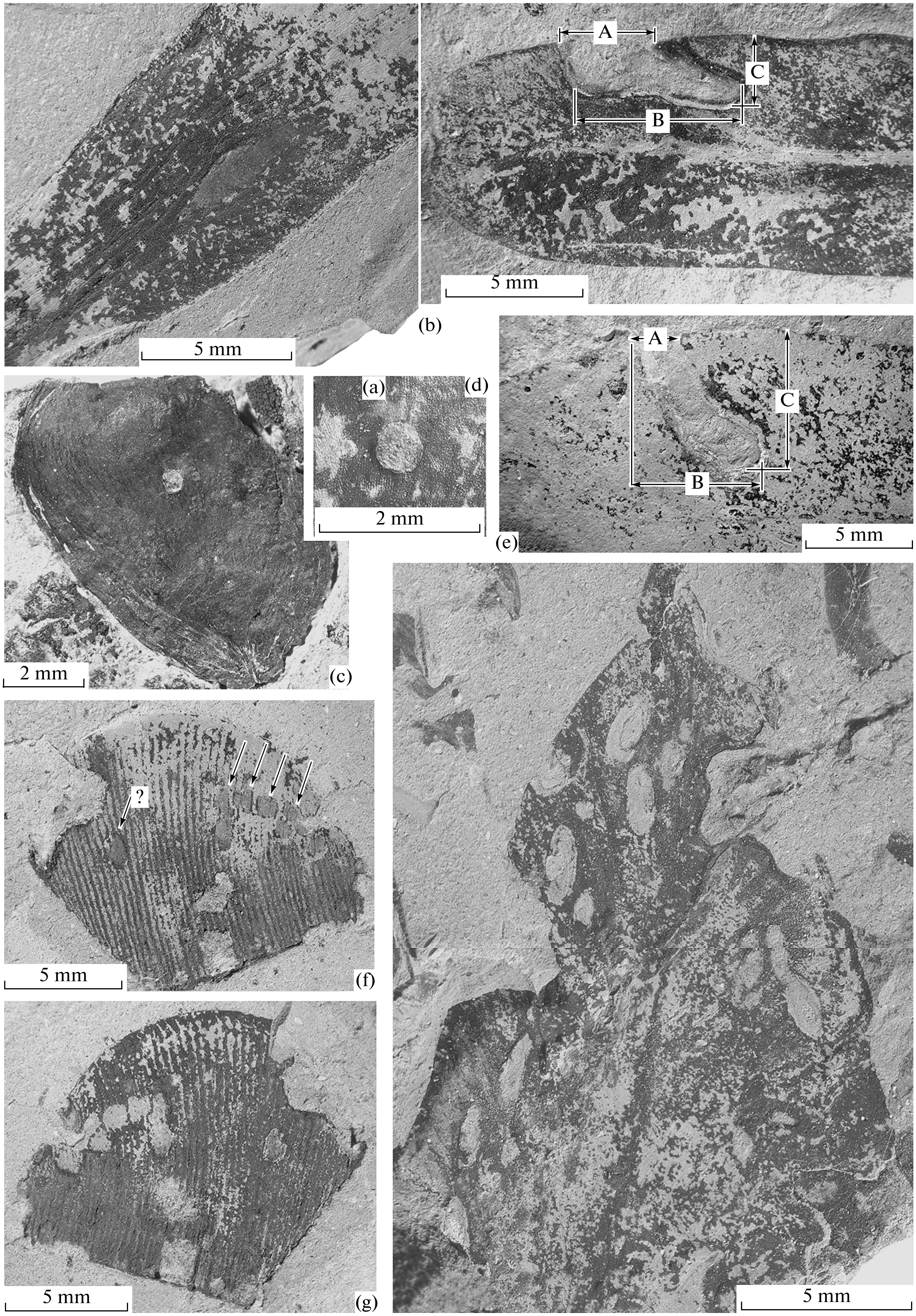
Taking into account the fact that the classification of marginal damage types is purely formal, the ratios of three main dimensions are used below in the descriptions of new forms (Figs. 9b, 9e): (*A*) maximum length of damage on external leaf margin (outline); (*B*) maximum length of internal part of damage (inside leaf outline); and (*C*) maximum depth of damage from the leaf blade edge. Comparison of these three parameters relative to each other characterizes the shape of traces and, along with the shape of the trace’s trajectory (straight, wavy, etc.), can be used for the description of species.

Family Phagophytichnidae Vjalov, 1975

Genus *Phagophytichnus* Amerom, 1966

Phagophytichnus sinitsae Vassilenko, sp. nov.

Etymology. In honor of the paleontologist S.M. Sinitsa.


5 mm
(b)
A
C
B
5 mm
A
C
B
5 mm
(e)
(a)
(d)
2 mm
2 mm
(c)
?
5 mm
(f)
5 mm
(g)
5 mm

Holotype. PIN, no. 3840/2402, feeding trace (marginal biodamage) on a leaf of *?Tatarina* sp.; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 9b). Local marginal damage of the leaf with a weakly wavy outline along line *B* and angles smoothly rounded with a large radius. *A* is considerably smaller than *B* and somewhat smaller than, or equal to, *C; B* is considerably longer than *C*. The injury does not reach the central part of the leaf.

Measurements, mm. $A = 3$; $B = 6$; $C = 2.5$.

Comparison. The new species differs considerably from *P. rectus* Vasilenko, 2007 and *P. ekowskii* Amerom, 1966 in the shape of the injury (*A* considerably smaller than *B*).

Material. Holotype.

Phagophytichnus farcimeniformis Vassilenko, sp. nov.

Etymology. From the Latin *farcimeniformis* (sausage-shaped).

Holotype. PIN, no. 3840/2652, feeding trace (marginal biodamage) on a leaf of *?Tatarina* sp.; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 9e). Local marginal damage of the leaf with a relatively straight outline along the line *C* and smoothly rounded along the line *B. A* is slightly smaller than, or equal to, *B; A* and *B* are considerably smaller than *C*. The injury does not reach the central part of the leaf.

Measurements, mm. $A = 1.5$; $B = 4.8$; $C = 5$.

Comparison. The new species differs from *P. rectus* and *P. ekowskii* in the shape of the injury (*A* is considerably smaller than *B*). It differs from *P. sinitsae* in the ratio of *A* to *C* (in *P. sinitsae, A* is slightly smaller than *C*; in *P. farcimeniformis,* it is considerably smaller).

Material. Holotype.

Traces of feeding on generative organs are the rarest type of damage found in the Isady locality. At present, only two specimens of *Salpingocarpus* sp. seeds (identified by E.V. Karasev, PIN) with traces of punctures have been studied (Figs. 9c, 9d). They are well pronounced medium-sized punctures about 0.5 mm in diameter. In the well preserved carbonized seed coat and in the counterpart, a slight thickening of the tissue along the injury margin is visible. The hole has a distinct even margin. The counterpart shows that the hole is filled with rock forming a distinct "column" (Fig. 9d).

Punctures in seeds often occur in the Upper Carboniferous and Lower Permian beds, but in the Upper Permian, they are obviously rare. Carboniferous and Permian punctures of seeds are traditionally attributed to palaeodictyopterans (Shcherbakov et al., 2009). The scarcity of both seeds with punctures and palaeodictyopteran fossils in Isady indirectly confirms this interpretation (in earlier deposits, both are significantly more abundant).

Endophytic ovipositions. One oviposition on a leaf fragment of *Pursongia* sp. was described from the Isady locality (Vassilenko, 2011). Another, poorly preserved specimen is probably a trace ("scar") from an oviposition of a closely related or the same species (Figs. 9f, 9g). The oviposition *Paleoovoidus rasnitsyni* Vassilenko, 2011 were probably introduced into leaf tissue by insects with elongate abdomens (as evidenced by the specific arcuate shape of the ovipositions). Vasilenko and Rasnitsyn (2007) have shown that Permian endophytic ovipositions could have belonged to kennedyine dragonflies, the ecological analogues of modern Zygoptera. Another specimen distinguished from the other known specimens by the egg arrangement on the leaf and by some other characters, is described below. It is uncertain whether or not the oviposition belongs to Odonata.

Family Paleoovoididae Vasilenko, 2005

Genus *Paleoovoidus* Vasilenko, 2005

Paleoovoidus ponomarenkoi Vassilenko, sp. nov.

Etymology. In honor of the paleoentomologist A.G. Ponomarenko.

Holotype. PIN, no. 3840/2401, oviposition on a leaf of *?Tatarina* sp.; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 9i). Medium-sized oval formations on a leaf blade, oriented from the leaf base to the apex, but not arranged strictly in one line. Elements of the oviposition are located along and near the leaf margins. The distance between separate elements in the presumably continuous series is at most 1 mm.

Measurements, mm. Length of the egg clutch, 20; egg length, 2.0; maximum egg width, 1.0; K = 2.0

Comparison. The new species differs from congeners in the weakly ordered arrangement of eggs and their tendency to be located closer to the leaf margin. In addition, it is distinguished by the proportions of eggs in the clutch; in the other species K = 2.5 or more.

Material. Holotype.

Fig. 9. New forms of evidence interactions between arthropods and plants from the Severodvinian Isady locality: (a) leaf gall of *Paleogallus krassilovi* Vassilenko, sp. nov., holotype PIN, no. 3840/2403; (b) feeding trace (marginal biodamage) of *Phagophytichnus sinitsae* Vassilenko, sp. nov., holotype PIN, no. 3840/2402; (c, d) *Salpingocarpus* sp. with a trace of puncture in the membrane; (f) feeding trace (marginal biodamage) of *Phagophytichnus farcimeniformis* Vassilenko, sp. nov., holotype PIN, no. 3840/2652; (f, g) endophytic oviposition of *?Paleoovoidus rasnitsyni* Vassilenko, 2011; (i) endophytic oviposition of *Paleoovoidus ponomarenkoi* Vassilenko, sp. nov., holotype PIN, no. 3840/2401.

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 Balymotikha localities) includes U-shaped structures on leaf blade margins and minelike formations rather similar in the type of tissue damage to ?*Phagophytichnus* 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 Balymotikha 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: ?*Tridelopterum indebitum* sp. nov. (Palaeomanteidae), *Epimastax mutovinensis* sp. nov. (Permosialidae), *Issapaloptera infracta* gen. et sp. nov., *Neembia ampla* gen. et sp. nov. (Permembiidae), and Jurinida: *Isadelytron speciosum* gen. et sp. nov., ?*Karajurina 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 *Mongolojurina* 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 interradial 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 *Paleuthygramma 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.

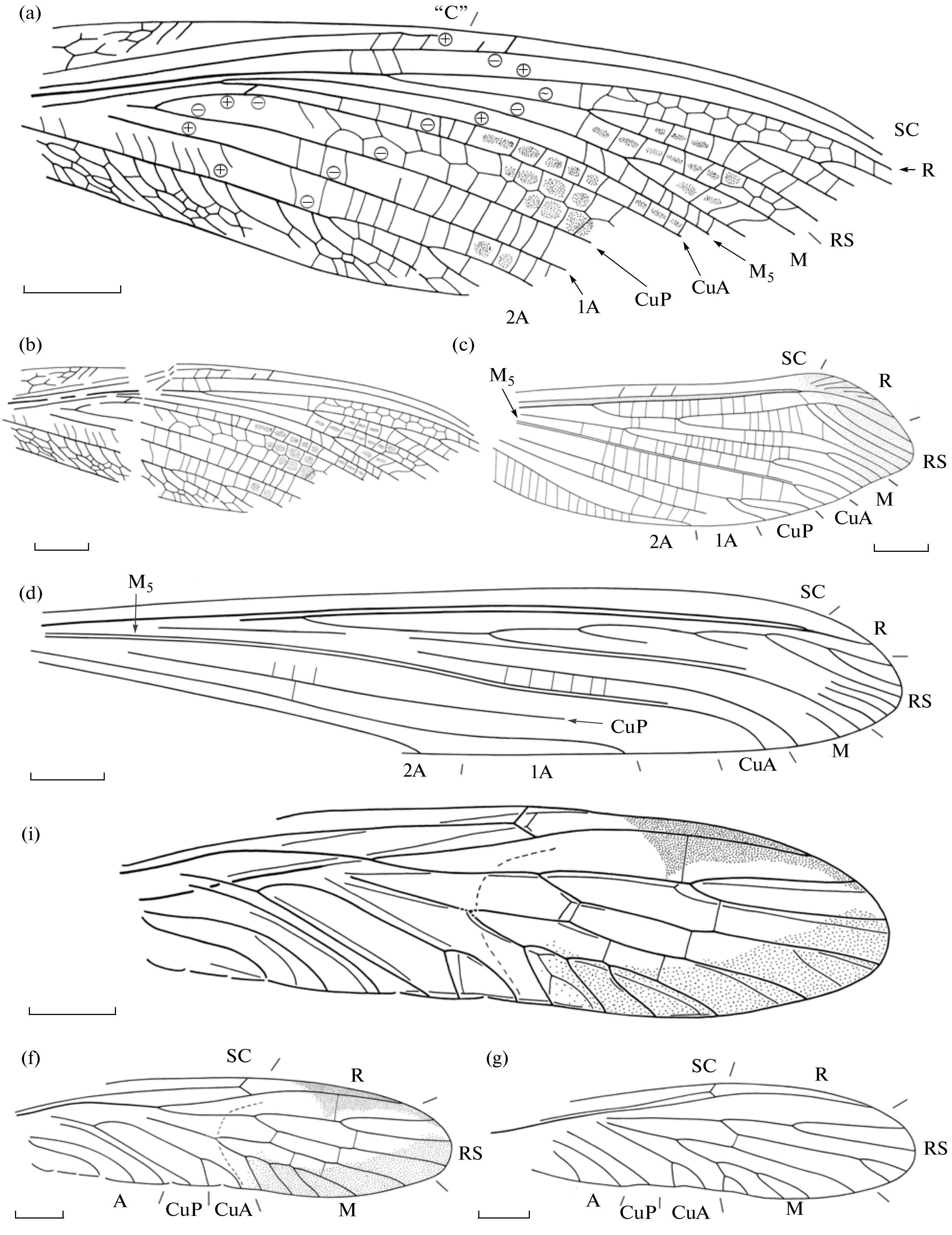
Type species. *I. issada* sp. nov.

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., *Permomerope* 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


(a)
"C"
SC
R
RS
M
M_5
CuA
CuP
1A
2A
(b)
(c)
SC
R
M_5
RS
M
CuA
CuP
1A
2A
(d)
M_5
SC
R
RS
CuP
M
CuA
1A
2A
(i)
(f)
SC
R
RS
A
CuP
CuA
M
(g)
SC
R
RS
A
CuP
CuA
M

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.

Etymology. From the village of Isady.

Holotype. PIN, no. 3840/1701, part and counterpart of incomplete forewing (without base); Isady locality, Vologda Region; Severodvinian Stage.

Description (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.

Measurements, mm. Length of preserved fragment, 7.4; width, 2.4; estimated forewing length, 8–9.

Material. Holotype.

Isadistica longa Rasnitsyn et Aristov, sp. nov.

Etymology. Feminine gender form of the Latin *longus* (long).

Holotype. PIN, no. 3840/684, part and counterpart of slightly distorted wing; Isady locality, Vologda Region; Severodvinian Stage.

Description (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).

Measurements, mm. Forewing length, 12.5; width, 1.9.

Comparison. 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.

Material. Holotype.

Order Hypoperlida Martynov, 1928

Family Hypoperlidae Martynov, 1928

Genus *Idelopsocus* Zalessky, 1929

Idelopsocus mutovinus Rasnitsyn et Aristov, sp. nov.

Etymology. From the Mutovino locality.

Holotype. PIN, no. 3840/1650, part and counterpart of overlapping, slightly distorted forewing and hindwing; Isady locality, Vologda Region; Severodvinian Stage.

Description (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.
Adiphlebiidae: 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; *Adiphlebia* 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 *Paracladus* 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 Ischnuroneuridae based on the following combination of characters of this genus, which make it similar to anthracoptilids 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 anteriad, 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-

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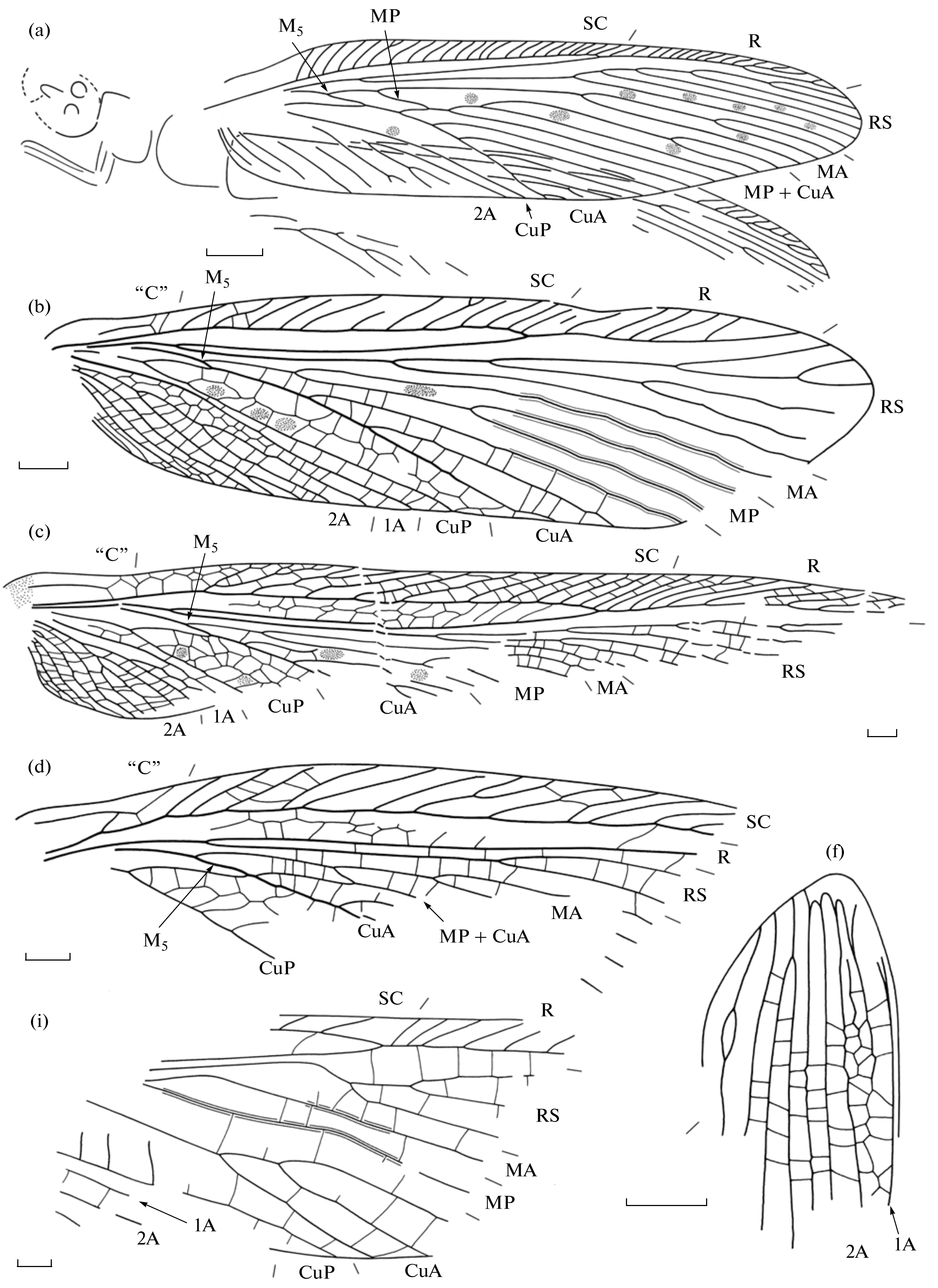
Fig. 11. Members of Hypoperlida: (a) *Ischnoneura oustaleti* (Brongniart,1885), holotype Muséum national d'histoire naturelle, DHT-R51077, habitus; Commentry locality, France; Stephanian Stage of the Upper Carboniferous (orig. drawing from photograph in Brongniart, 1885, tabl. XXI, fig. 4); (b–d) *Strephoptilus* gen. nov., Isady locality, Vologda Region; Severodvinian 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.


(a)
M$_5$
MP
SC
R
RS
MA
MP + CuA
2A
CuP
CuA
(b)
"C"
M$_5$
SC
R
RS
MA
MP
2A
1A
CuP
CuA
(c)
"C"
M$_5$
SC
R
RS
MA
MP
CuA
CuP
1A
2A
(d)
"C"
SC
R
RS
MA
MP + CuA
CuA
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RS
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MP
1A
2A
CuP
CuA

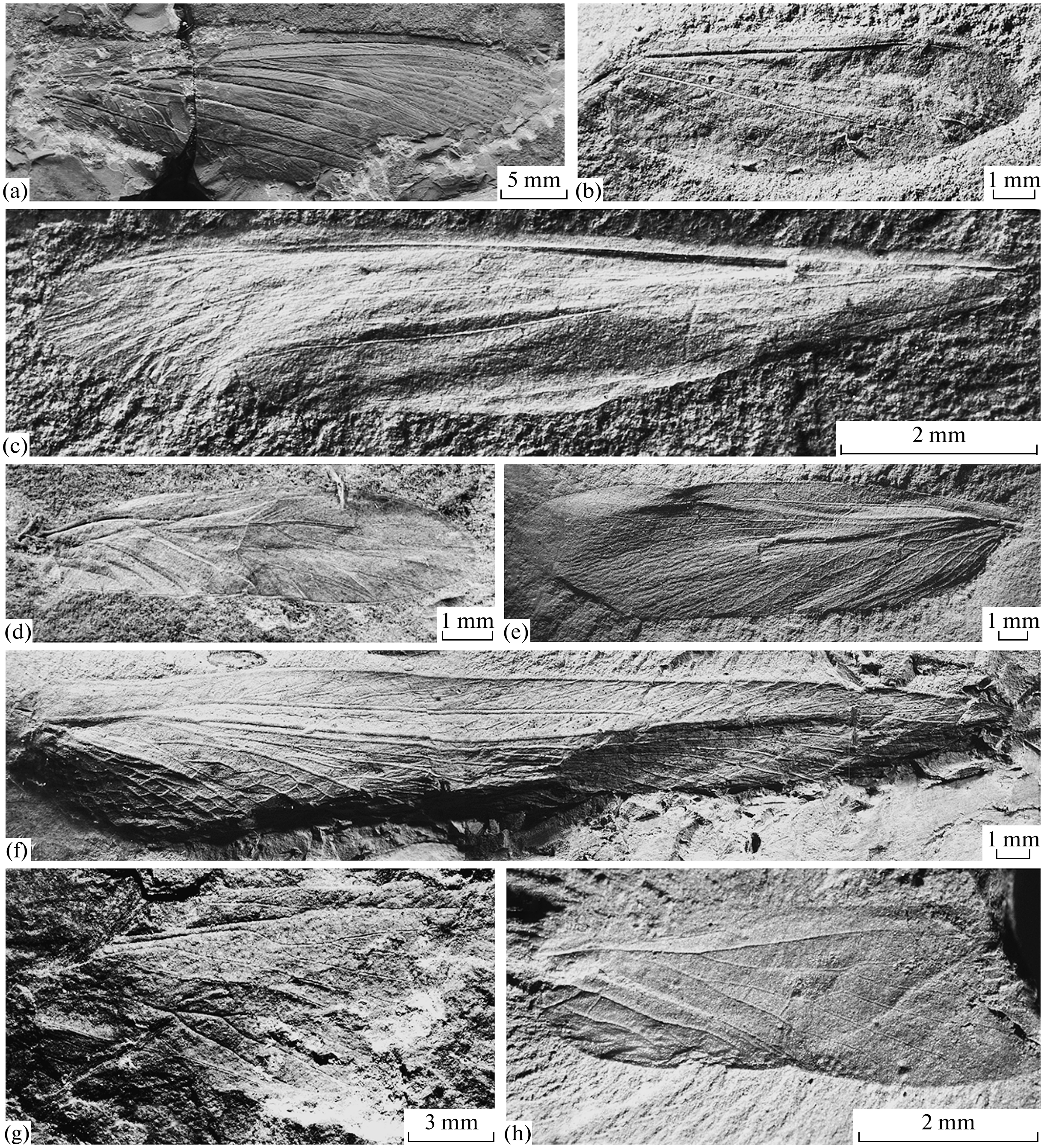

Fig. 12. Members of Caloneurida, Hypoperlida, and Palaeomanteida: (a) *Eohymen maculipennis* Martynov, 1937, holotype PIN, no. 100/2, forewing; Kargala locality, Orenburg Region; Urzhumian Stage; (b) *Isadistica issada* sp. nov., holotype PIN, no. 3840/1701, forewing; Isady locality, Vologda Region; 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 CuA_2 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 paleodyctiopteroids (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, M_5. 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; Severodvinian 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 M_5; MA is simple; MP is free, with a bifurcation. CuA is pectinate anteriad, 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.

Etymology. From the Latin *longus* (long).

Holotype. PIN, no. 3840/1652; part and counterpart of forewing without apex and most of posterior margin; Isady locality, Vologda Region; Severodvinian Stage.

Description (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).

Measurements, mm. Length of incomplete forewing, 31; estimated total length, about 33–35.

Comparison. 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.

Remarks. 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).

Material. 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.

Etymology. The Latin *patiens* (patient).

Holotype. PIN, no. 3286/134; part and counterpart of incomplete forewing clavus; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (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.

Measurements, mm. Length of fragment, 4.7; width of clavus near base, 2.5.

Comparison. 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).

Remarks. 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 *Adiphlebia 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 polyneurous.

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. Zalessky, 1929 (Zalessky, 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.

Material. 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.

Etymology. 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 (=Palaeomanteida), 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 Permembiidae, recently transferred to this order from Grylloblattida (Aristov and Rasnitsyn, 2008). The traditional miomotperans, 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. Zalessky, 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 Permembiidae, 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_5) 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 Permembiidae 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 (normally, distal to middle of anal space); CuA with bifurcation.

Generic composition. *Palaeomantis* Handlirsch, 1906, *Delopterum* Sellards, 1909, *Miomatoneura* Martynov, 1927, *Delopsocus* Tillyard, 1928, *Sellardsiopsis* G. Zalessky, 1939, *Miomatoneurella* O. Martynova, 1958, *Permonia* Kukalová, 1963, *Perunopterum* Kukalová, 1963, *Permodelopterum* Kukalová, 1963, *Saaromioptera* Guthörl, 1963, *Palaeomantina* Rasnitsyn, 1977, *Delopterinus* Rasnitsyn in Rasnitsyn et al., 2004, *Neodelopterum* Rasnitsyn in Rasnitsyn et al., 2004, *Stigmodelopterum* Rasnitsyn in Rasnitsyn et al., 2004, and *Tridelopterum* 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 Permembiidae 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 interradial and radiomedial 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 angulately 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; CuA_1 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 *?Tridelopterum* Rasnitsyn in Rasnitsyn et al., 2004

?Tridelopterum 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).

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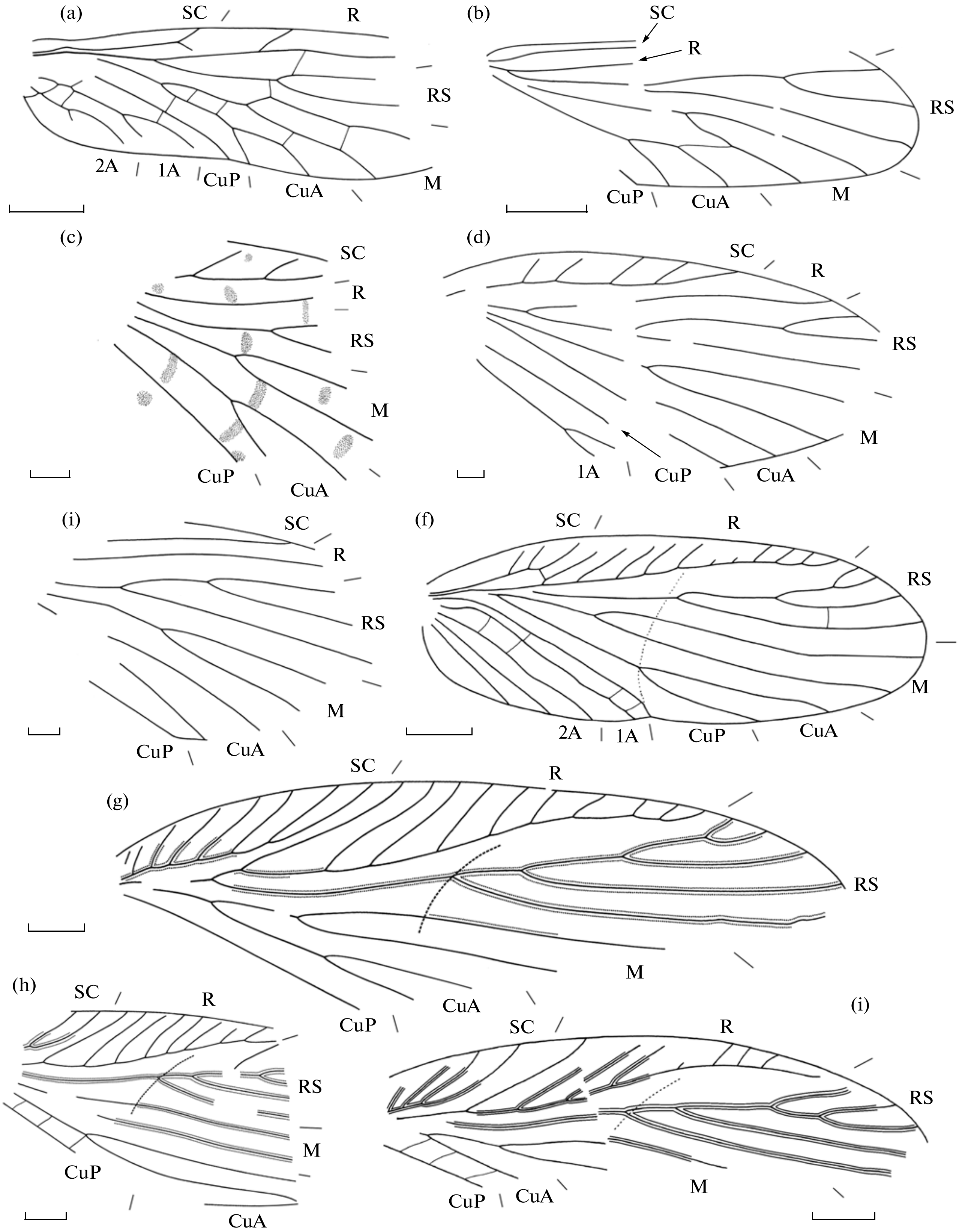
Fig. 13. Members of the families Palaeomanteidae and Permosialidae (Palaeomanteida): (a) *?Miomatoneurella rossoshana* sp. nov., holotype PIN, no. 3286/119, forewing; Udmurtia, Chepanikha locality, Urzhumian Stage; (b) *?Tridelopterum indebitum* sp. nov., holotype PIN, no. 3840/1029, hindwing; Isady 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.


(a)
SC
R
RS
2A
1A
CuP
CuA
M
(b)
SC
R
RS
CuP
CuA
M
(c)
SC
R
RS
M
CuP
CuA
(d)
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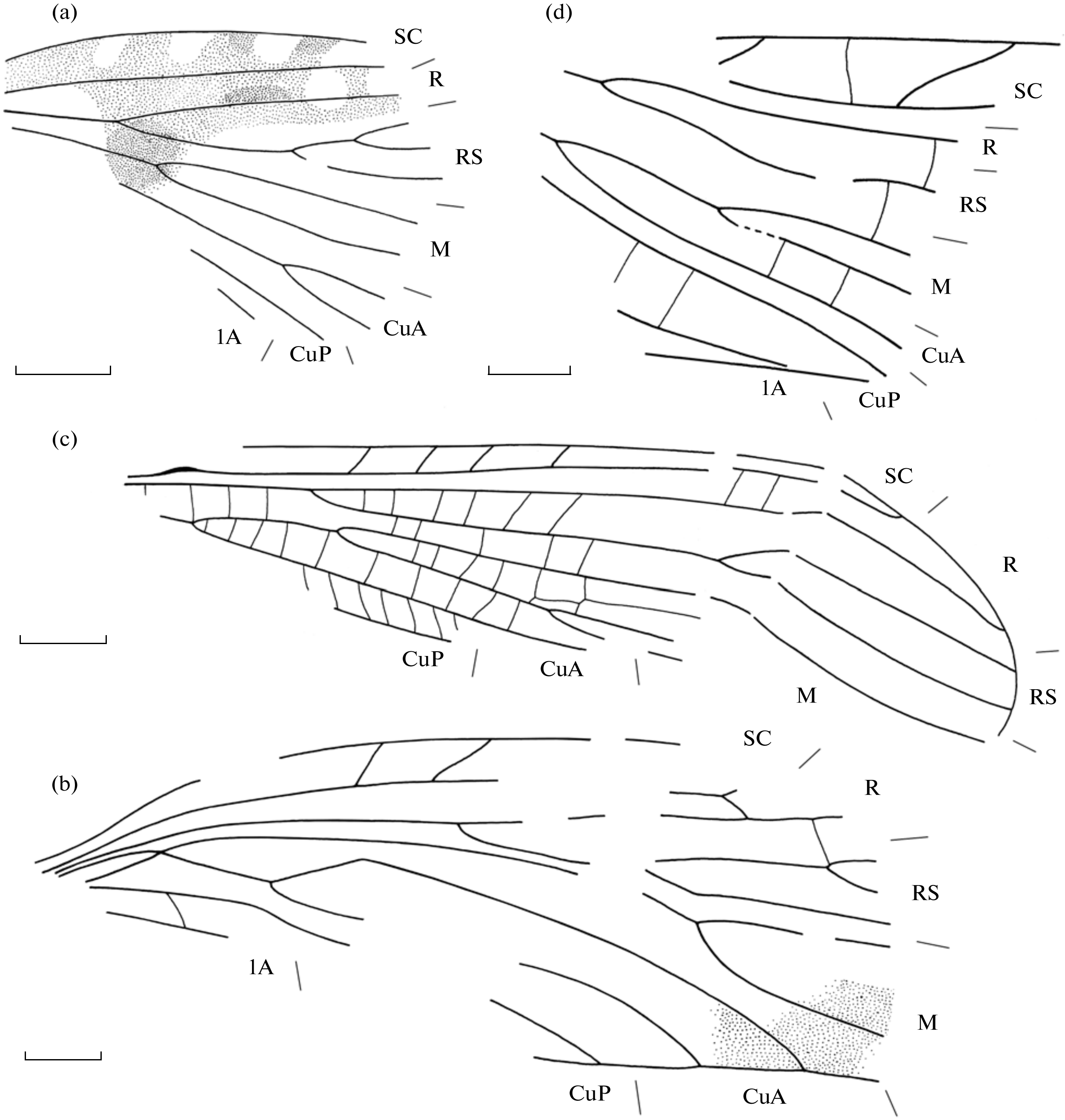

Fig. 14. Members of the families Permosialidae and Permembiidae (Palaeomanteida), forewings: (a) *Balymotikha deterior* sp. nov., holotype PIN, no. 5103/20, Vyazniki locality, Vladimir Region; Vyatkian Stage; (b) *Onthomastax coprinus* sp. nov., holotype PIN, no. 3286/146, Chepanikha locality, Udmurtia; 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 segment 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 Permembiidae by the absence of a long M + CuA, and from Permembiidae 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. frivolus* 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 RS_{1+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. frivolus* (Storozhenko, 1991) (Storozhenko and Novokshonov, 1999, text-figs. 5, 6), but it is considerably smaller in size: at the level of the apex of CuA_2, 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 preradial 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 RS_1. 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.

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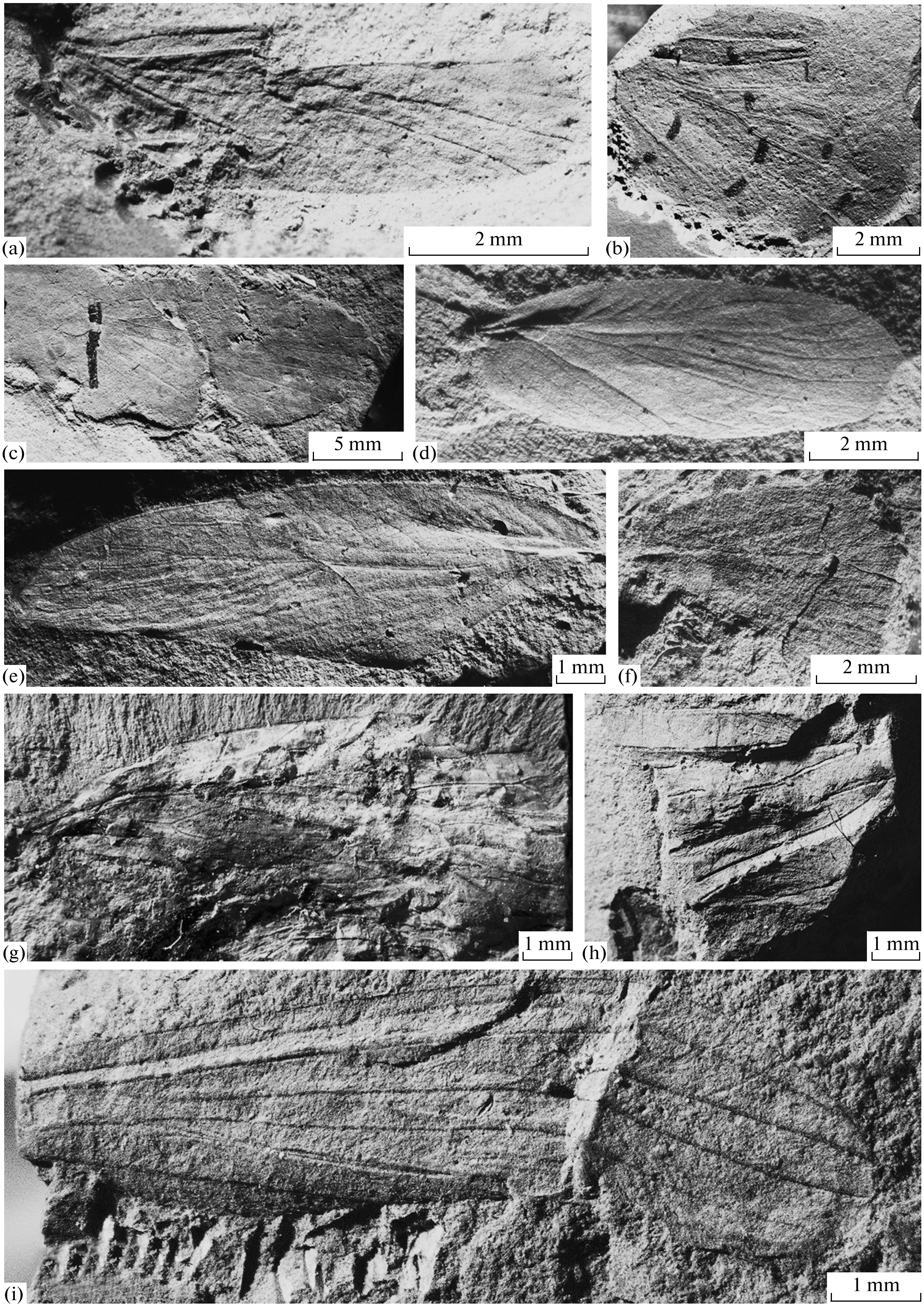
Fig. 15. Members of the families Palaeomanteidae and Permosialidae (Palaeomanteida): (a) *?Tridelopterum indebitum* sp. nov., holotype PIN, no. 3840/1029, hindwing; Isady locality, Vologda Region; Severodvinian Stage; (b) *Permosialis zavialovensis* sp. nov., holotype PIN, no. 3286/124, forewing; Chepanikha 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.


(a)
2 mm
(b)
2 mm
(c)
5 mm
(d)
2 mm
(e)
1 mm
(f)
2 mm
(g)
1 mm
(h)
1 mm
(i)
1 mm

Epimastax mutovinensis Rasnitsyn et Aristov, sp. nov.

Etymology. From the Mutovino locality.

Holotype. PIN, no. 3840/1660, part and counterpart of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (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.

Measurements, 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).

Comparison. The new species is similar to *E. tshepanikha* 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).

Remarks. 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*.

Material. 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.

Etymology. From the Balymotikha locality. Gender feminine.

Type species. *B. deterior* sp. nov.

Diagnosis. 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.

Species composition. Type species.

Comparison. 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.

Remarks. 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.

Etymology. The Latin *deterior* (inferior).

Holotype. PIN, no. 5103/20, direct impression of incomplete forewing of mediocre preservation; Balymotikha locality, Vladimir Region; Vyatkian Stage.

Description (Figs. 14a, 15f). The forewing is probably broadly darkened, with many light spots and a dark spot in the interradial, radiomedial, and mediocubital 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 subcostal 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 anteriad, 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 anteriad and towards the wing apex.

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

Material. Holotype.

Family Permembiidae 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 *Permembia* 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 Permembiidae, 3.4), about 19.

Material. Holotype.

Order Jurinida M. Zalessky, 1929

Remarks. The order Jurinida, or Glosselytrodea, 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,*

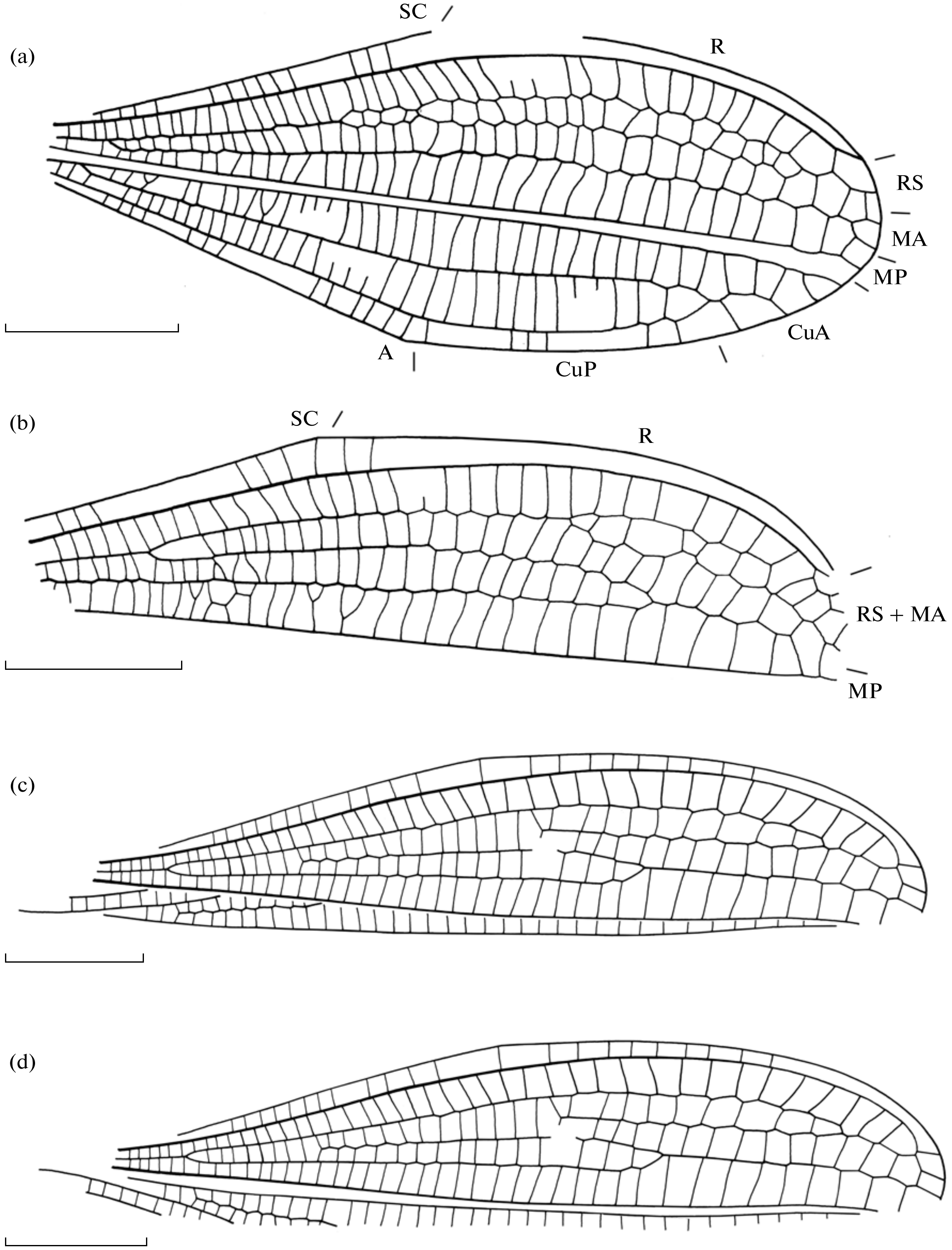


Fig. 16. *Eoglosselytrum biarmicum* sp. nov. (Jurinida: Jurinidae), forewings; Chepanikha locality, Udmurtia; Urzhumian Stage: (a) holotype PIN, no. 3286/120; (b) paratype PIN, no. 3286/121; (c, d) paratype PIN, no. 3286/138: (c) preserved venation; (d) reconstruction.

"G." linguale, Polycytella, etc. Therefore, we are compelled to reject opposing Polycytellidae 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-

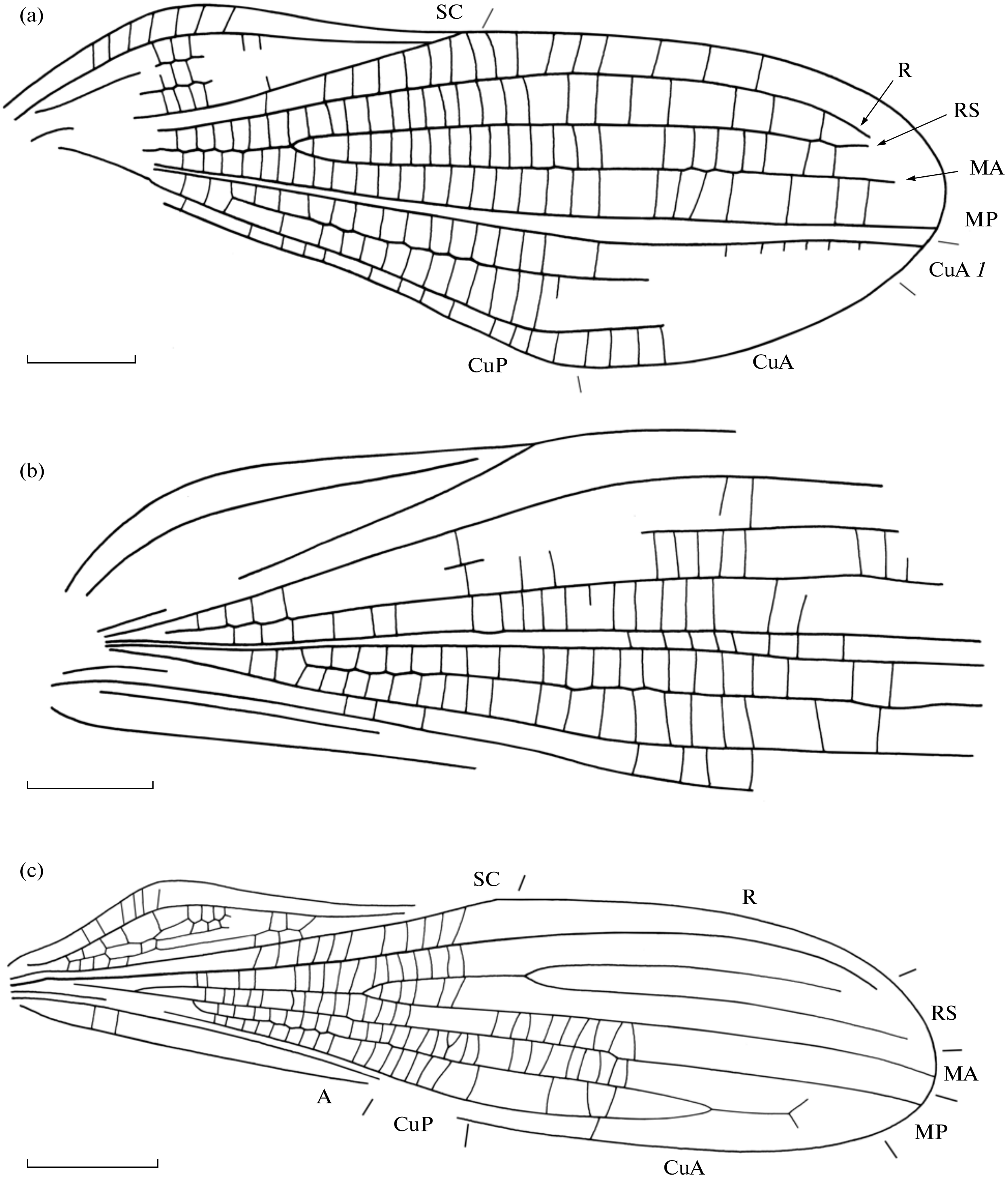


Fig. 17. Members of the family Jurinidae (Jurinida), forewings: (a, b) ?*Eoglosselytrum kultshumovense* sp. nov., Kul'chumovo locality, Orenburg Region; Severodvinian Stage: (a) holotype PIN, no. 5273/26; (b) paratype PIN, no. 5273/25; (c) *Isadelytron speciosum* sp. nov., holotype PIN, no. 3840/443, 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. Zalessky, 1929, judging from the bet-

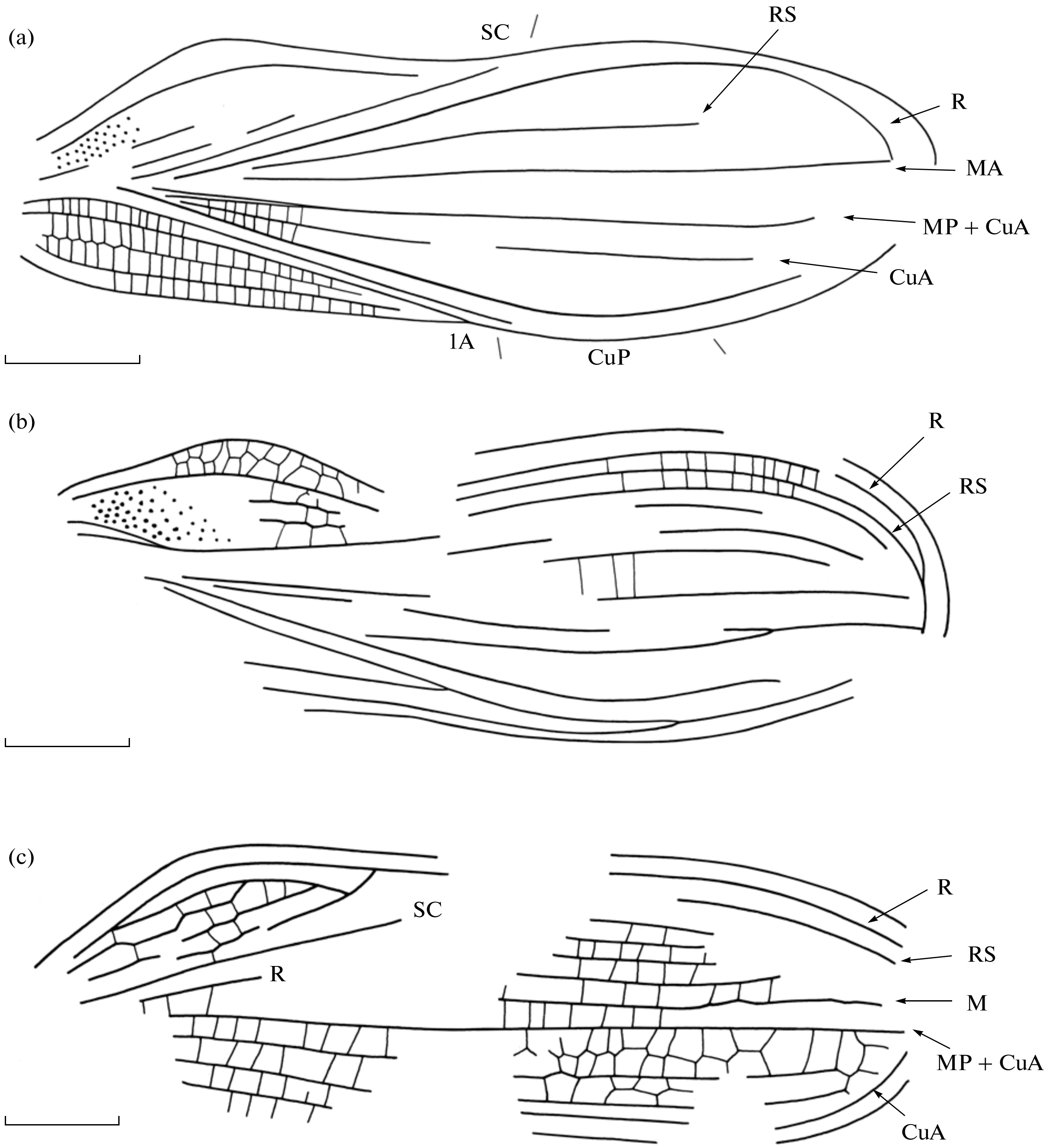


Fig. 18. Members of the families Jurinidae and Glosselytridae (Jurinida), forewings: (a, b) *?Isadelytron planum* sp. nov.; Chepanikha locality, Udmurtia; Urzhumian Stage: (a) holotype PIN, no. 3286/136; (b) paratype PIN, no. 3286/137; (c) *?Karajurina desperata* sp. nov., holotype PIN, no. 3840/398; 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 distinguishing 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, *Mongolojurina* 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. Zalessky, 1929, comprising of *Jurina* M. Zalessky, 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 *Mongolojurina* 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. Zalessky, 1929

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

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

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

Type genus. *Jurina* M. Zalessky, 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

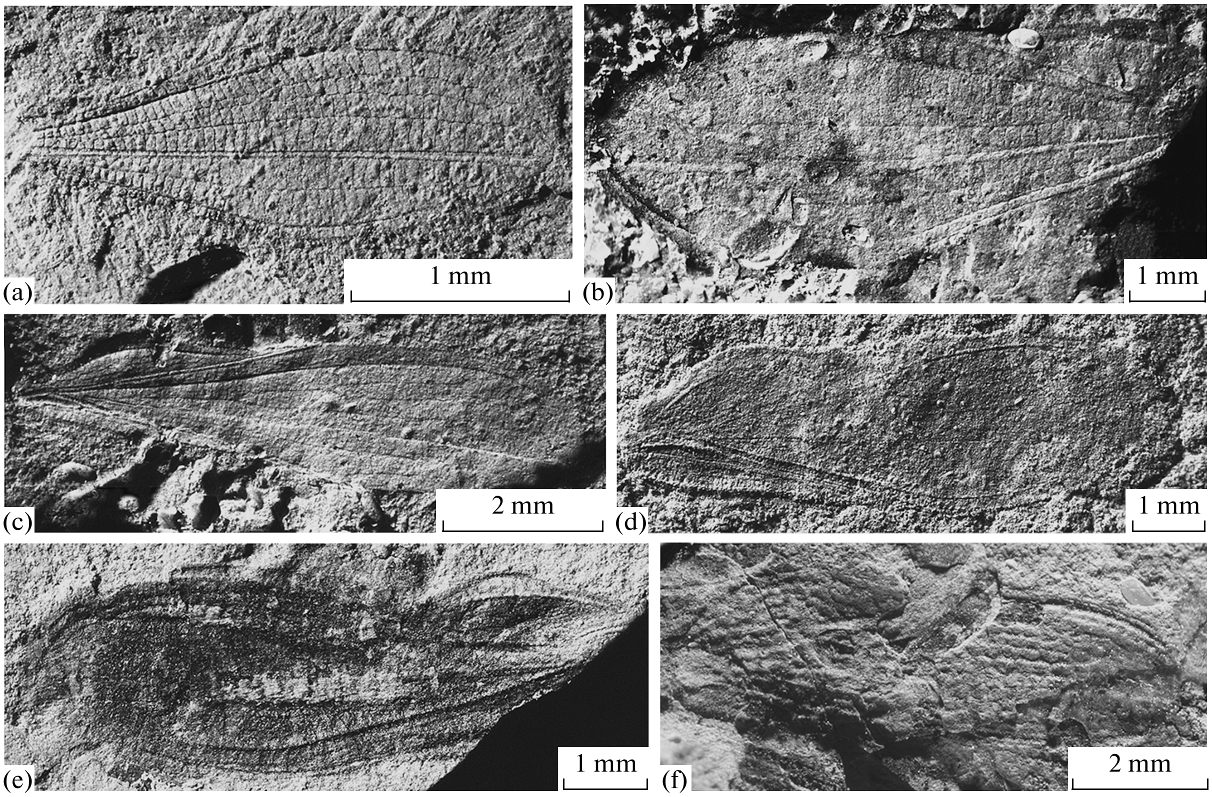


Fig. 19. Members of the families Jurinidae and Glosselytridae (Jurinida), forewings: (a) *Eoglosselytrum biarmicum* sp. nov., holotype PIN, no. 3286/120, Chepanikha locality, Udmurtia; Urzhumian Stage; (b) *?Eoglosselytrum kultshumovense* sp. nov., holotype PIN, no. 5273/26, Kul'chumovo locality, Orenburg 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.

Polycytellidae: Martynova, 1952, p. 189 (type genus *Polycytella* 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, *Polycytella* 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, *Mongolojurina* 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 *Karoohymen* 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 paleoentomologist 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

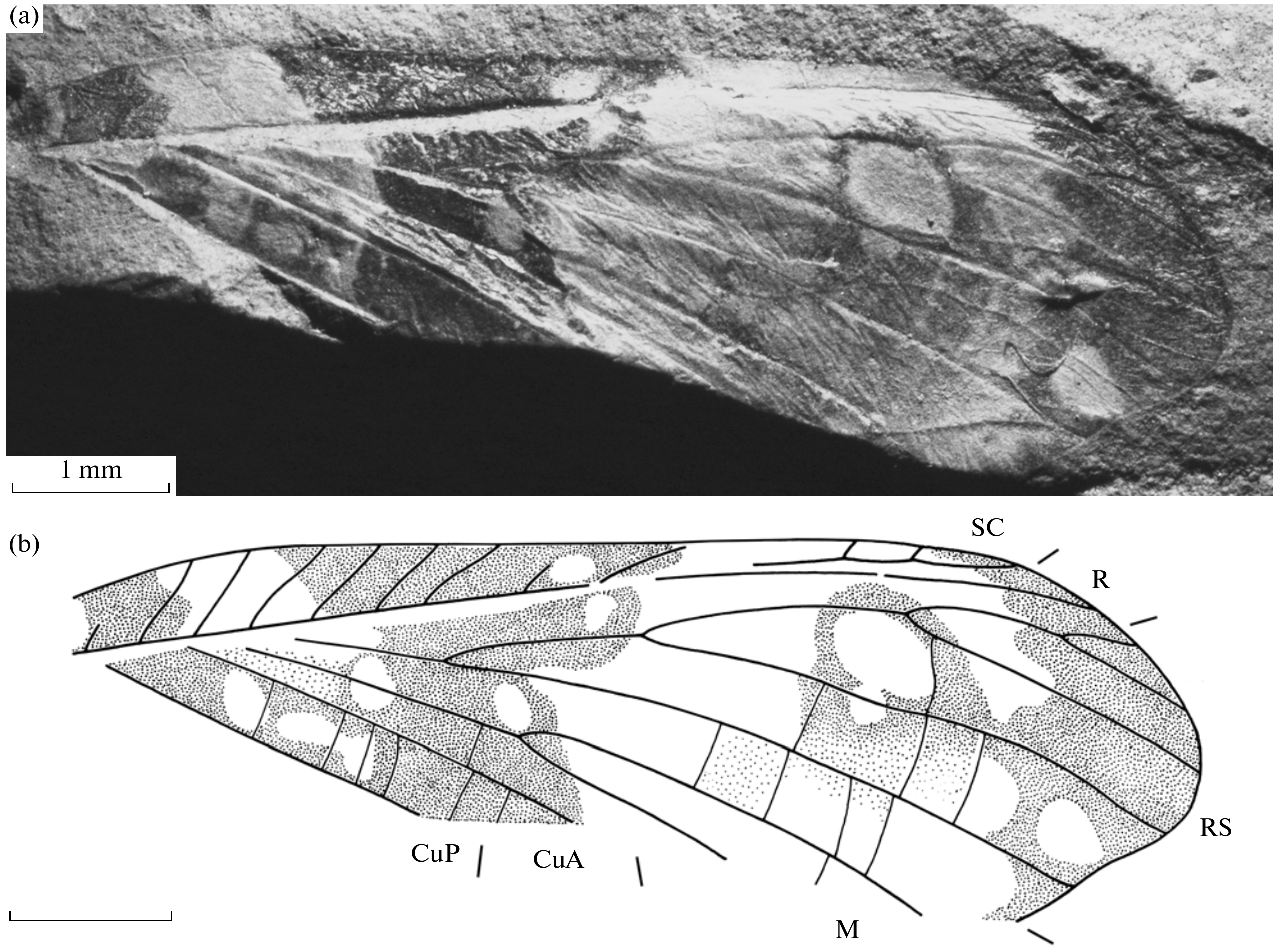

Fig. 20. *Issadohymen ponomarenkoi* gen. et sp. nov. (Mischopterida: Moravohymenidae), holotype PIN, no. 3840/799, fore- or hindwing; Isady locality, Vologda Region; Severodvinian Stage. Scale bar, 1 mm.

forks, the distance between its branches is almost twice that between MA and MP. The wing has distinct spots of vague shape.

Measurements, mm. Length of preserved wing fragment, 19.5; total wing length, about 22.

Remarks. The wing margin between the posterior branches of RS seems slightly concave; this is probably a crumpled part of the wing, formed in the course of fossilization, rather than a wavy wing margin found in some Mischopterida.

Material. Holotype.

2.3. New Beetles (Insecta, Coleoptera) from the Latter Half of the Permian of European Russia

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In this chapter, 53 beetle specimens are described, collected recently in Permian deposits of the European Russia and assigned to the families Permocupedidae, Taldycupedidae, Permosynidae, Asiocoleidae, Rhombocoleidae, and Schizocoleidae. Two genera and 34 species are newly described. Most of the specimens are isolated elytra, the position of which in the natural system is often undetermined and, hence, they are described in the formal system. Nevertheless, it turned out that changes in morphological types of the elytra followed certain patterns. A total of 13 Middle and Upper Permian beetle localities are known in European Russia. Temporal changes in elytral assemblages are divided into five stages. The dominance shifted from permocupedids to schizophoroids; then, permocupedids disappeared; taldycupedids emerged; permosynids emerged; and then, by the terminal Permian, permosynids acquired the major role. Permosynids may include members of both Adephaga and Polyphaga, two major groups of Mesozoic–Cenozoic beetles.

The data on Permian beetles have recently noticeably increased, although they remain poorly understood because examination of this material is labor consuming. The correlation potential of beetles is

Triassic	Lower	Induan	Nedubrovo
Permian	Upper	Vyatkian	Vyazniki Aristovo ?Kul'chumovo
		Severodvinian	Isady Babintsevo Novo-Aleksandrovka
	Middle	Urzhumian	Kargala Chepanikha, Kostovaty
		Kazanian	Kityak Soyana Tikhie Gory

Fig. 21. Stratigraphic position of localities accepted in this study.

extremely high, but their usage is hindered by insufficient understanding. Previously, a more or less complete sequence of Middle and Late Permian beetles was only known from the Kuznetsk Basin. As a result of recent expeditions, the sequence of oryctocoenoses of European Russia containing beetle fossils has become more complete, but many localities have yielded too few beetle fossils to make reliable conclusions. Therefore, what is said below should be taken for preliminary consideration. A total of about 155 fossil beetle specimens from the Middle and Upper Permian of European Russia have been collected; 53 of them are treated in this study. As a result, two new genera and 34 new species are described and several specimens are identified as previously described species (Martynov, 1937; Ponomarenko, 1963, 1969, 2000b, 2003, 2004). The diversity of beetles at the end of the Permian was rather high; the majority of species are described from a single specimen. Schisophoroids were the most diverse group; permocupedids were least diverse, represented by the greatest number of repeated finds.

In eastern European Russia, Middle and Late Permian beetles have been found in 13 localities from the Lower Kazanian to Vyaznikian deposits, terminal for the Permian (Vyazniki Stage according to Lozovskii and Kukhtinov, 2007). The stratigraphic positions of localities accepted here is shown in Fig. 21. Six localities are known from the Biarmian Series of the Permian: three Kazanian and three Urzhumian. Seven are known from the Tatarian Series: two Severodvinian, two Vyatkian, two Vyaznikian localities, and one (Kul'chumovo) probably Early Vyatkian. The number of known Siberian beetle localities of this age is approximately the same. In other regions of the world, Middle and Late Permian beetles have only been found in nine localities: three in South Africa, two in Mongolia, two in China, one in South America, and one in Australia. The composition of beetles found in these localities characterizes five stages of their changes. Note that beetle fossils are rare in localities of European Russia (Ponomarenko, 2000b, 2004). The abundance of beetles becomes somewhat higher only at the very end of the Permian, especially in localities of the terminal Permian (Vyazniki).

According to the stratigraphy accepted by the Interdepartmental Stratigraphic Committee of Russia, the Biarmian corresponds to the Guadalupian and the Tatarian corresponds to the Lopingian of the International Scale; however, it is possible that only the Vyatkian Stage and, perhaps, the very beginning of the Severodvinian Stage correspond to the Lopingian. This correlation (Newell at al., 2010, Kotlyar, 2010) complies better with the main stages of beetle evolution (Ponomarenko, 2010). The beetles found in China, in deposits previously dated Lower Lopingian (Lin, 1982) and now considered to be terminal Capitanian (Lin et al., 2010), correspond to Severodvinian rather than Urzhumian beetles.

Beetle remains have not been recorded in Ufimian deposits of either the Pechora Basin or Cis-Ural Region, although, in the latter region, they have been found in the Kungurian. However, the Ufimian beds have yielded too small insect sample s to include necessarily rare beetles of that time. In the Lower Kazanian beds of European Russia, beetles are almost as rare as in the Lower Permian. Beetles (and many other insect groups) found in the Lower and Upper Kazanian differ considerably in taxonomic composition. The most primitive and almost exclusively Early Permian family Tshekardocoleidae is represented in the Middle Permian by one specimen from the Lower Kazanian Soyana locality, Arkhangelsk Region (Ponomarenko, 2000b). Remaining beetles from this locality belong to the family Permocupedidae, but to the genus *Permocupes*, which is rather advanced in elytral morphology. The diversity of beetles from Soyana does not increase with the growth of collections from this locality; almost all new specimens belong to the most frequent species *P. sojanensis* Ponomarenko, 1963. The asymmetrical occurrence pattern usually suggests that the most abundant species have already been collected. This situation can hardly be regarded as accidental, since beetles from the Tikhie Gory locality (Tatarstan), which is similar in age, but geo-

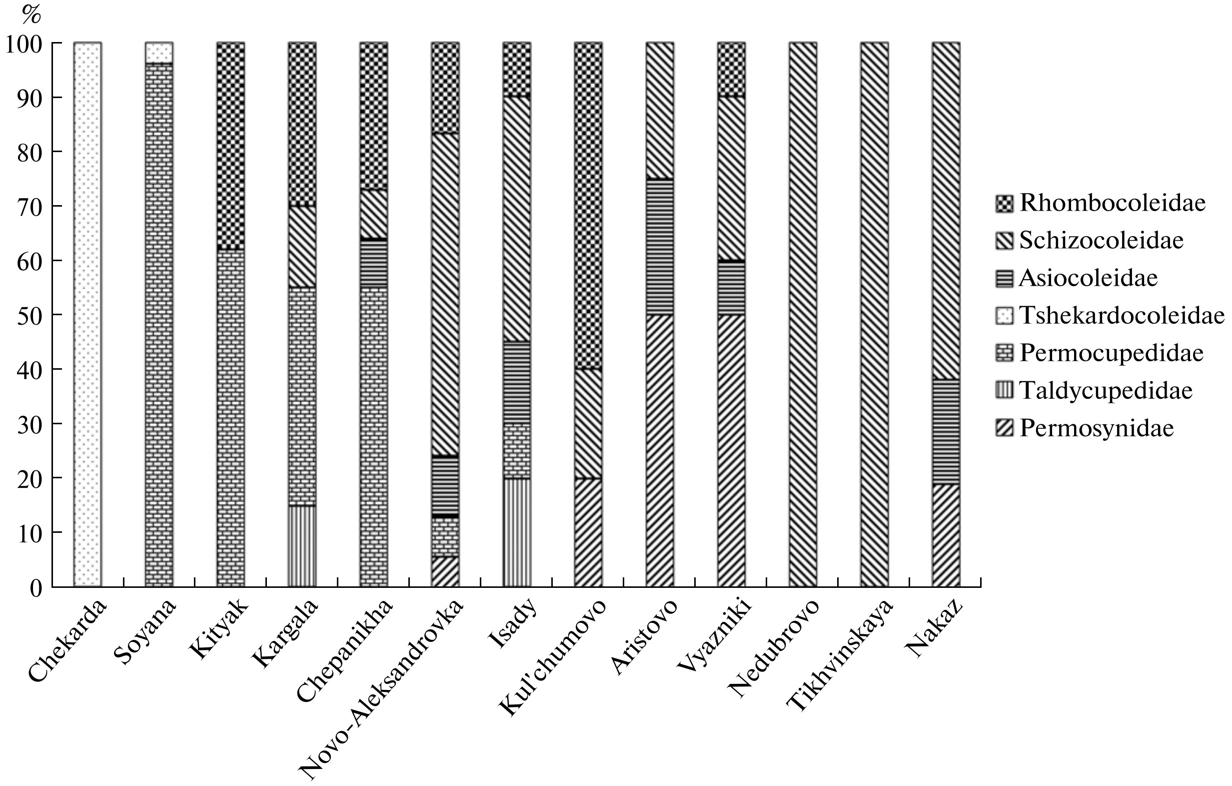


Fig. 22. Percentage of fossil Coleoptera of identified families found in different localities.

graphically remote, also belong to this genus. Upper Kazanian and Urzhumian beetles are similar in elytral morphology. The family Permocupedidae is dominant; fossil beetles of more advanced types are rare and belong mostly to schizophoroids (Rhombocoleidae and Schizocoleidae); they only slightly increased in abundance during the Late Kazanian and Urzhumian. The cupedoid branch is represented even more poorly. Beetle assemblages from the three Urzhumian localities differ strongly. In Kargala and Chepanikha, permocupedids compose about half of specimens, while, in Kostovaty, they have not been found, although Chepanikha and Kostovaty are situated close to each other and believed to be of the same age. In Kargala, one specimen of Taldycupedidae has also been found. However, Urzhumian specimens on the whole comply well with the trend of changes in the composition of beetles.

The number of Severodvinian localities is three; two of them have yielded representative collections. In Novo-Aleksandrovka, 15 fossils have been found: a single permocupedid and 14 schizophoroids. In the Isady locality, 39 specimens have been found, surprisingly including , four permocupedids, possibly representing beetles of the same species; four specimens belong to Taldycupedidae; two belong to Asiocoleidae; three belong to Rhombocoleidae; and especially many (13) belong to Schizocoleidae. In Babintsevo, only one schizocoleid has been found. Beetles from the Kul'chumovo locality, which is possibly of the Vyatkian age, include one permosynid; others are schizophoroids. Late Vyatkian and Vyaznikian beetles are dominated by Schizocoleidae and Permosinidae, which at least partly belong to the higher suborder Polyphaga. Infrequent Asiocoleidae have also been found here. This family was only represented by a single specimen from the Permian of the Kuznetsk Basin, but presently available material is rather diverse, so that they have closed the gap between this family and Tricoleidae, which was previously known from the Upper Triassic. Very recently, beetle elytra have been found in Vyazniki deposits, terminal for the Permian of European Russia (Ponomarenko, 2011). Ostracodes collected here include typical Triassic forms (Lozovskii and Kukhtinov, 2007); the earliest known Pseudosuchians have also been found here, although the general pattern of the assemblage remains Permian. The compositions of beetles in each locality are given below; the proportions of families are shown in Fig. 22.

List of Beetles Found in Particular Localities

The localities are given below according to the stratigraphic sequence, from the earliest to latest. Detailed stratigraphic and geographic positions are given for those localities the specimens from which are described in this study, see Chapter 1.

Vyazniki (Sokovka and Balymotikha). Vladimir Region, environs of the town of Vyazniki; Upper Permian, Vyatkian Stage, Zhukovian Horizon, *Archosaurus rossicus* Zone.

Permosynidae: *Hydrobiites tillyardi* Ponomarenko, 2011, *H. vladimiri* Ponomarenko, 2011, *Permosyne rasnitsyni* Ponomarenko, 2011.

Asiocoleidae: *Tetracoleus sennikovi* Ponomarenko, 2011.

Rhombocoleidae: *Erunakicupes angustus* Ponomarenko, 2011.

Schizocoleidae: *Uscatocoleus rhinchophorus* Ponomarenko, 2011, *U. eurypygus* Ponomarenko, 2011, *Pseudochrysomelites major* Ponomarenko, 2011, *Metrorhynites baculum* Ponomarenko, 2011, *M. elongatus* Ponomarenko, 2011.

Aristovo. Vologda Region, Velikoustyugskii District, right bank of the Northern Dvina River, 0.5 km upstream from the village of Aristovo; Upper Permian, Vyatkian Stage, Upper Vyatkian Substage, Salarevo Formation, Komaritsa Member; *Scutosaurus karpinskii* Zone, *Chroniosuchus paradoxus* Subzone.

Permosynidae: *Permosyne europaeum* Ponomarenko, 2003, *P. incertum* Ponomarenko, 2003.

Schizocoleidae gen. sp.

Asiocoleidae: *Tetracoleus permianus* Ponomarenko, sp. nov.

Kul'chumovo. Orenburg Region, Saraktashskii District, right bank of the Sakmara River, 3 km downstream from the village of Kul'chumovo, second gully from Kul'chumovo; Upper Permian, ?Vyatkian Stage.

Permosynidae: *Sakmaracoleus orenburgensis* Ponomarenko, sp. nov.

Rhombocoleidae: *Aenigmocoleus uralensis* Ponomarenko, sp. nov., *Rossocoleus sakmara* Ponomarenko, sp. nov.

Schizocoleidae: *Schizocoleus major* Ponomarenko, sp. nov.

Isady. Vologda Region, Velikoustyugskii District, left bank of the Sukhona River, 1 km upstream from the village of Isady; Upper Permian, Severodvinian Stage, Poldarsa Formation, lower part of the Kalikino Member, *Proelginia permiana* Zone, *Chroniosaurus levis* Subzone.

Permocupedidae: *Protocupoides esini* Ponomarenko, sp. nov.

Taldycupedidae: *Taldycupes cellulosus* Ponomarenko, sp. nov.; *Simmondsia permiana* Ponomarenko, sp. nov.

Asiocoleidae: *Bicoleus laticella* Ponomarenko, sp. nov.; *Tetracoleus tricoleoides* Ponomarenko, sp. nov.

Rhombocoleidae: *Karakanocoleus mutovinensis* Ponomarenko, sp. nov.; *Erunakicupes grossus* Ponomarenko, sp. nov., *Rossocoleus aristovi* Ponomarenko, sp. nov.

Schizocoleidae: *Schizocoleus depressus* Ponomarenko, sp. nov.; *Uskatocoleus micron* Ponomarenko, sp. nov., *U. sukhonenis* Ponomarenko, sp. nov., *U. convexus* Ponomarenko, sp. nov.; *Pseudochrysomelites bashkuevi* Ponomarenko, sp. nov., *P. sphenoidalis* Ponomarenko, sp. nov., *P. medialis* Ponomarenko, sp. nov., *P. longus* Ponomarenko, sp. nov.

Babintsevo. Orenburg Region, Grachevskii District, right slope of the gully, right tributary of the Konduzla River, 2.8 km northeast of the village of Babintsevo; Upper Permian, Severodvinian Stage, Upper Severodvinian Substage, *Deltavjatia vjatkensis* Zone, *Chroniosaurus dongusensis* Subzone.

Schizocoleidae: *Uscatocoleus uralensis* Ponomarenko, sp. nov.

Novo-Aleksandrovka. Orenburg Region, Sarapul'skii District, left bank of the Kuplya River near the village of Novo-Aleksandrovka, 6 km from the village of Troitskoe; Upper Permian, Severodvinian Stage, Vyazovka Formation.

Permocupedidae: *Tatarocoleus granulatus* Ponomarenko, 2004.

Asiocoleidae: *Tetrocoleus orenburgensis* sp. nov., *Bicoleus cuplensis* sp. nov.

Rhombocoleidae: *Rhombocoleus gomankovi* sp. nov., *Karakanocoleus europeus* Ponomarenko, 2004; *Erunakicupes brevis* Ponomarenko, 2004.

Schizocoleidae: *Schizocoleus longus* Ponomarenko, 2004, *S. glabrus* Ponomarenko, 2004, *S. minimus* sp. nov., *Pseudochrysomelites ovum* (Ponomarenko. 2004), *P. robustus* (Ponomarenko, 2004).

Chepanikha. Republic of Udmurtia, Zav'yalovskii District, upper part of the gully open from the left into the Rossokha River near the village of Chepanikha; Middle Permian, Urzhumian Stage, *Ulemosaurus svijagensis* Zone.

Permocupedidae: *Protocupoides elongatus* Ponomarenko, sp. nov., *Permocupes latus* Ponomarenko, sp. nov.

Rhombocoleidae: *Rossocoleus novojilovi* Ponomarenko, sp. nov., *R. angustus* Ponomarenko, sp. nov.

Kostovaty. Republic of Udmurtia, Votkinskii District, right bank of the Kama River 6.4 km downstream from Galevo dock; Middle Permian, Urzhumian Stage, *Ulemosaurus svijagensis* Zone.

Asiocoleidae: *Schizotaldycupes pubescens* Ponomarenko, sp. nov.

Rhombocoleidae: *Rhombocoleites uralensis* Ponomarenko, sp. nov.

Kargala. Orenburg Region, Sakmarskii District, dumps of Kargala copper mines; Middle Permian, Urzhumian Stage, Amanak Formation, *Estemmenosuchus uralensis* Zone.

Rhombocoleidae: *Curculiopsis ellipticus* Martynov, 1937, *Rhombocoleites adumbratus* Ponomarenko, 1969.

Permocupedidae: *Kaltanicupes kargalensis* Ponomarenko, 1963.

Taldycupedidae: *Tecticupes martynovi* sp. nov.

SYSTEMATIC PALEONTOLOGY

Fossil beetles described below come from Middle and Upper Permian localities of European Russia. Almost all of them are represented by isolated elytra and described in formal taxa. Some beetles from these beds have already been described (Martynov, 1937, Ponomarenko, 1963, 1969, 2000b, 2003, 2004), but the material collected recently expands considerably our knowledge of Late Permian Coleoptera.

Family Permocupedidae Martynov, 1933

Genus *Permocupes* Martynov, 1933

The species described below is assigned to the genus *Permocupes* because of its compliance with the diagnosis of this genus: main cubital and anal veins (two main veins closest to suture) fused near apex; subcostal (external) field of elytron with three rows of cells; dilated base of cubital field with four rows of cells; other fields with two rows each.

Permocupes latus Ponomarenko, sp. nov.

Plate 1, fig. 1

Etymology. The Latin *latus* (wide).

Holotype. PIN, no. 3286/46, direct impression of left elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Fig. 23). The elytron is relatively small, flattened, rather wide, thrice as long as wide, very weakly dilated from the base, and narrowed in the apical quarter; its apex is acute, asymmetrical; the sutural margin is bordered. The epipleural rim is very wide, with two rows of cells. The cells are rounded; each row contains about 40 cells. The main veins are sharply different from the intermediate veins; the intermediate veins are zigzagging; the basal part of the third (cubital) vein is strongly oblique. Two main veins closest to the suture are fused in the apical quarter of the elytron, and the resulting common vein extends into the elytral apex.

Measurements, mm. Elytral length, 3.6; elytral width, 1.2.

Comparison. In the presence of the common cubital–anal vein and the small size, the new species is similar to *P. semenovi* Martynov, 1933 and differs from it and all other species in the wide elytron and very wide epipleural rim.

Material. Holotype and paratypes PIN, nos. 3286/139, 140, 141, 143, and 145: incomplete elytra from the same locality.

Genus *Protocupoides* Rohdendorf, 1961

The species described below are assigned to the genus *Protocupoides* because of their compliance with its diagnosis: main veins not fused near apex; subcostal (external) field of elytron with three rows of cells; dilated base of cubital field with four rows of cells; other fields with two rows of cells. Anal (closest to suture) main vein of elytron almost reaching elytral apex.

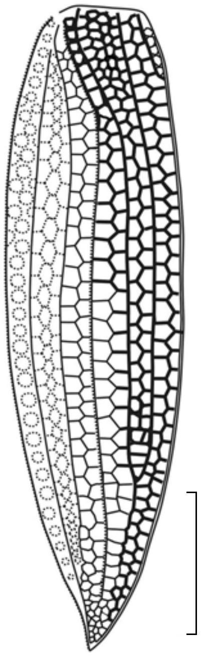


Fig. 23. *Permocupes latus* sp. nov., holotype PIN, no. 3286/46, elytron; Chepanikha locality, Udmurtia; Urzhumian Stage. Scale bars in Figs. 23–27, 1 mm.

Protocupoides elongatus Ponomarenko, sp. nov.

Plate 1, fig. 2

Etymology. The Latin *elongatus* (elongate).

Holotype. PIN, no. 3286/45, part and counterpart of left elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Fig. 24). The elytron is convex, elongate, 4.7 times as long as wide, weakly dilated from the base and narrowed in the apical one-third; its apex is acute, symmetrical, protruding as a “tail”; the sutural margin is bordered. The epipleural rim is narrow. The cells are rounded rectangular; each row contains about 40 cells. The subcostal field has three rows of cells almost over the entire length of the field. The main veins are clearly different from the intermediate veins; the intermediate veins are straight; the basal part of the third (cubital) vein is strongly oblique. Both rows of cells behind the last not shortened (anal) vein are almost equal in length. The basal vein closest to the suture is curved towards the sutural margin near the apex. Elytral cells do not form regular transverse rows. Shortened scutellar vein reaches the sutural margin of the elytron.

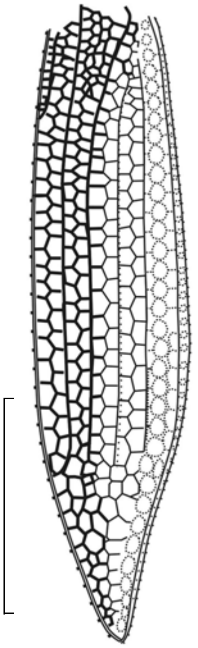


Fig. 24. *Protocupoides elongatus* sp. nov., holotype PIN, no. 3286/45, elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

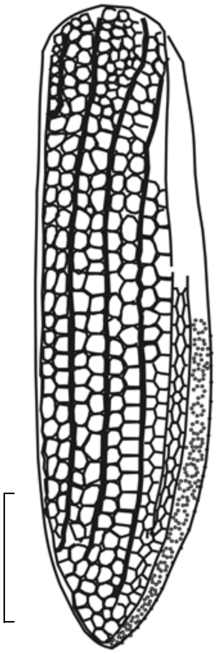


Fig. 25. *Protocupoides esini* sp. nov., holotype PIN, no. 3840/28, elytron; Isady locality, Vologda Region; Severodvinian Stage.

Measurements, mm. Elytral length, 3.8; elytral width, 0.8.

Comparison. In the almost equally long rows of cells along the sutural margin and in the subcostal field, almost straight intermediate veins, the main vein closest to the suture curved towards the sutural margin, and rounded rectangular shape of cells, the new species is particularly similar to *P. acer* Rohdendorf, 1961 and differs from it in the less elongate cells and in the elytral apex protruding as a "tail."

Material. Holotype.

***Protocupoides esini* Ponomarenko, sp. nov.**

Plate 1, fig. 3

Etymology. In memory of the paleoichthyologist I.O. Esin, one of the first paleontologists to study the Isady locality.

Holotype. PIN, no. 3840/28, direct impression of right elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 25). The elytron is convex, elongate, 3.7 times as long as wide, dilated from the base and narrowed in the apical one-third; its apex is rounded, symmetrical; the sutural margin is bordered. The epipleural rim is narrow. The cells are rounded rectangular; each row contains about 35 cells. The subcostal field has three rows of cells extending almost throughout the field length. The main veins are only slightly different from the intermediate veins; the intermediate veins are straight; the basal part of the third (cubital) vein is strongly oblique. Both rows of cells behind the last nonshortened (anal) vein closely approach its apex. The elytral cells form almost regular transverse rows. The shortened scutellar vein reaches the sutural margin of the elytron.

Measurements, mm. Elytral length, 3.6; elytral width, 0.4.

Comparison. In the almost equally long rows of cells along the sutural margin and in the subcostal field and the rounded rectangular shape of cells, the new species is particularly similar to *P. acer* Rohdendorf, 1961 and differs from it in the only slightly different main and intermediate veins, the less elongate cells, and the blunt and rounded elytral apex.

Remarks. Due to only slightly differing main and intermediate veins and almost regular transverse rows of cells, the new species can be mistaken for a member of Taldycupedidae, but, in contrast to this family, its main veins differ somewhat from the intermediate veins.

Material. Holotype and paratypes PIN, nos. 3840/437, 1282: incomplete elytra from the same locality.

Family Taldycupedidae Rohdendorf, 1961

Genus *Tecticupes* Rohdendorf, 1961

The species described below is assigned to the genus *Tecticupes* because of its compliance with the diagnosis of this genus: main veins not fused near apex,

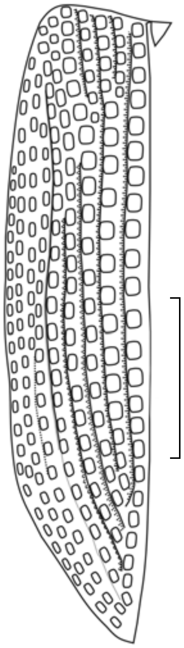


Fig. 26. *Tecticupes martynovi* sp. nov., holotype PIN, no. 199/158a, pattern of cells on elytron; Kargala locality, Orenburg Region; Urzhumian Stage.

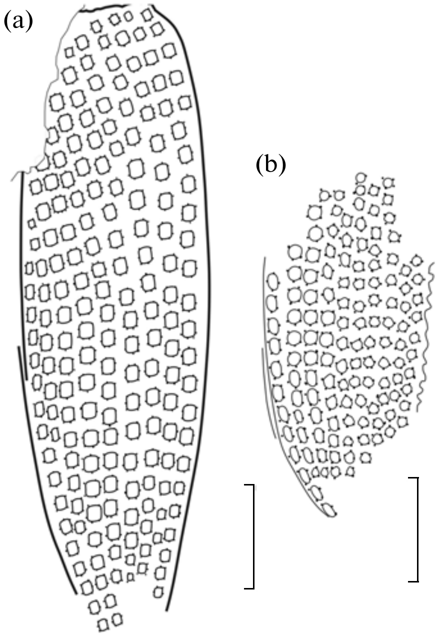


Fig. 27. *Taldycupes cellulosus* sp. nov., elytra; Isady locality, Vologda Region; Severodvinian Stage: (a) holotype PIN, no. 3840/438; (b) paratype PIN, no. 3840/436.

dilated base of cubital field with only three rows of cells, and other fields with two rows of cells. Short scutellar vein terminating short of reaching posterior margin of elytron and joining preceding vein.

Tecticupes martynovi Ponomarenko, sp. nov.

Plate 1, fig. 4

Etymology. In honor of A.V. Martynov, the founder of Russian paleoentomology, who was the first to describe Permian beetles.

Holotype. PIN, no. 199/158a, direct impression of paired elytra, external fields crumpled by flattening of the fossil; Kargala locality; Middle Permian, Urzhumian Stage.

Description (Fig. 26). The elytron is flattened, elongate, 4.8 times as long as wide, weakly dilated from the base and narrowed in the apical one-third; its apex is acute, asymmetrical, shifted towards the sutural margin; the sutural margin is bordered. The epipleural rim is very narrow. The cells are rounded rectangular, often arranged into transverse rows; each row contains about 25 cells. The veins are straight, the basal part of the third (cubital) vein is weakly curved. Both rows of cells behind the last nonshortened (anal) vein closely approaches its apex. The shortened scutellar vein does not reach the sutural margin of the elytron.

Measurements, mm. Elytral length, 3.7; elytral width, 0.7.

Comparison. The new species differs from *T. heckeri* Rohdendorf, 1961 in the two not shortened veins closest to the sutural margin not fused near the apex; it differs from *T. indistinctum* Rohdendorf, 1961 in the larger size and in the fact that these veins curve towards the sutural margin near their apices.

Material. Holotype.

Genus *Taldycupes* Rohdendorf, 1961

The species described below are assigned to the genus *Taldycupes* because of their compliance with its diagnosis: main veins not fused near apex, subcostal (external) field of elytron with three rows of cells, dilated base of cubital field with four rows of cells, other fields with two rows of cells. Anal (scutellar) main vein closely approaching elytral apex.

Taldycupes cellulosus Ponomarenko, sp. nov.

Plate 1, figs. 5 and 6

Etymology. The Latin *cellulosus* (cellular).

Holotype. PIN, no. 3840/438, direct impression of left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 27). The elytron is relatively narrow, convex, 3.5 times as long as wide, narrowing in the apical one-third; its apex is symmetrical. The epipleural rim is narrow. The cells are rounded tetragonal, much wider than the veins; each row contains about 25 cells. The longitudinal veins are zigzagging, reach-

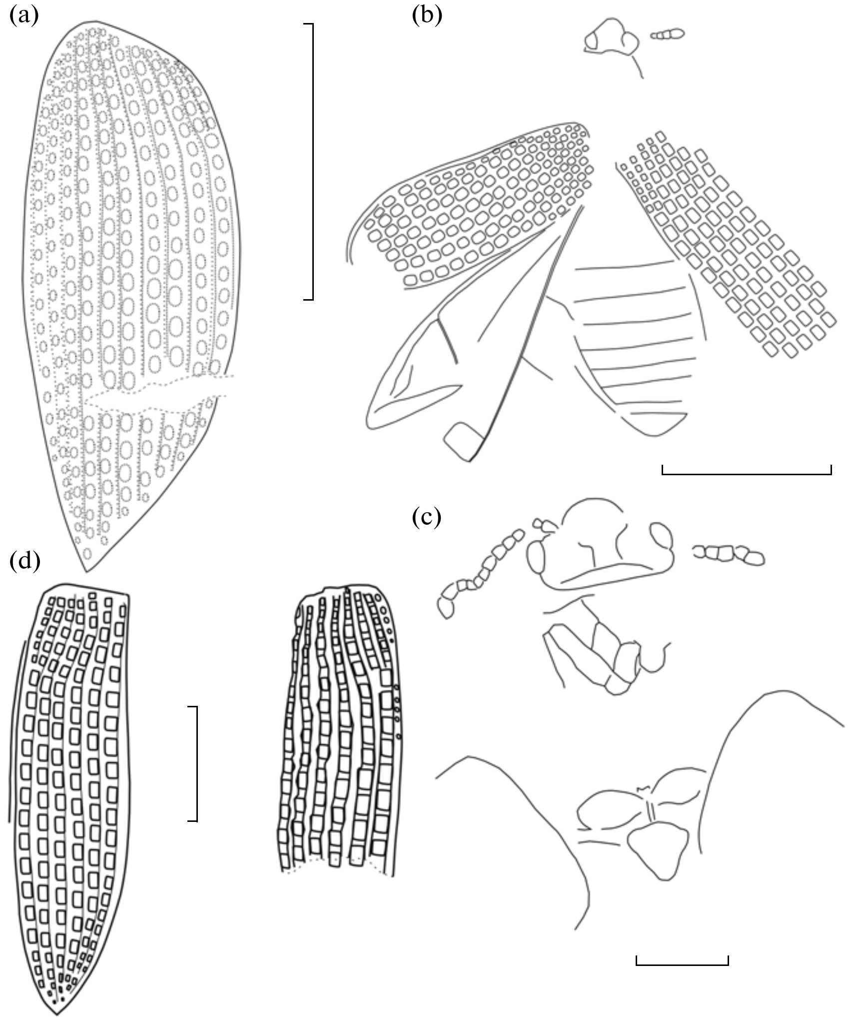


Fig. 28. *Simmondsia permiana* sp. nov.; Isady locality, Vologda Region; Severodvinian Stage: (a) holotype PIN, no. 3840/1602; (b) paratype PIN, no. 3840/688. Scale bars: (a, b, d) 0.2 and (c) 0.5 mm.

ing the elytral margin. The shortened rows of cells in the cubital field are long and contain up to seven cells. There are five cells behind 3A.

Measurements, mm. Elytral length, 5.8; elytral width, 2.3.

Comparison. The new species belongs to species with rounded cells and zigzagging longitudinal veins. It is distinguished by the longer shortened rows of cells in the cubital field.

Material. Holotype and paratypes PIN, nos. 3840/436, 686: elytra from the same locality.

Genus *Simmondsia* Dunstan, 1924

The new species describe below is assigned to the genus *Simmondsia* because it lacks additional short rows of cells at the base of the cubital field.

Several beetle fossils from the Isady locality belong to this species, including one almost complete beetle and several isolated elytra. The material include wide elytra with ten rows of cells and narrow elytra with six rows of cells. All of them are very similar in shape, patterns of cells and ribs between them, and the absence of shortened rows of small cells at the elytral base, a character rarely observed in Permian beetles. This suggests that the beetles initially had the same elytral morphology, with an almost vertical external field. In the course of fossilization, the external fields of some elytra were unfolded and became accessible for study, while, in others, they were compressed and no traces of them have been preserved (for more detail, see Ponomarenko, 1969, p. 8, text-fig. 3). One isolated unfolded elytron was designated as the holotype, while a more complete specimen is not, because it has incomplete narrow elytra. It is noteworthy that the only previously described Permian beetle that was assigned to this genus, *Simmondsia ragosini* (Rohdendorf, 1961), also has incomplete elytra without external fields (Ponomarenko, 1969, p. 123, text-fig. 69).

Simmondsia permiana Ponomarenko, sp. nov.

Plate 1, figs. 8a and, 8b

Etymology. From the Permian period.

Holotype. PIN, no. 3840/1602, direct impression of left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 28). A small beetle. The elytron is strongly convex, in the unfolded state, 3.5 times as long as wide, narrowed in the apical one-third; its apex is symmetrical. The epipleural rim is narrow. The cells are rounded tetragonal, rarely almost oval, and much wider than the veins; each row contains about 20 cells. Unfolded elytra have ten rows of cells; narrowed elytra have six to seven. Longitudinal ribs (veins) are straight, almost symmetrically reaching the elytral margins. There are five cells behind 3A.

The head is subtriangular, widest in the area of the temples, has mandibles of approximately equal length and width; ; the genae and eyes are shorter than the temples. The eyes are convex, positioned on the sides of the head. The gular sutures are short, widely set. The pronotum is transverse, slightly narrowed posteriad, slightly more than half as long as the head. The abdomen is narrowed beginning from the base of the second ventrite; the apical ventrite is almost twice as long as the penultimate ventrite.

Measurements, mm. Body length, about 2.2; elytral length, 1.9–2.1; width of unfolded elytron, about 1; width of narrowed elytron, 0.5–0.6.

Comparison. The new species belongs to species with subrectagonal cells and straight longitudinal ribs; it differs from them in the very small size and in the sutural veins extending almost into the elytral apex rather than the posterior elytral margin.

Remarks. The study of specimens is complicated by their small size and the type of enclosing rock.

Material. In addition to the holotype, paratypes PIN, no. 3840/688 (almost complete beetle) and isolated elytra, PIN, no. 3840/1279 (unfolded) and PIN, no. 3840/1703 (narrowed), from the same locality.

Family Permosynidae Tillyard, 1924

The family is a formal taxon, combining isolated elytra of Permian and Triassic beetles complying with the following diagnosis: elytron with 7 to 14 longitudinal grooves, including short scutellar groove and groove bordering elytral margin. Grooves usually punctured.

Genus *Sakmaracoleus* Ponomarenko, gen. nov.

Etymology. From the Sakmara River and the latinized Greek *koleos* (sheath).

Type species. *Sakmaracoleus orenburgensis* sp. nov.

Diagnosis. Elytron convex, elongate, parallel-sided, only slightly dilated from base and narrowed only in apical quarter. Middle of elytron with 11 puncture grooves. Medially, base of elytron with two shortened veins between fourth and fifth nonshortened veins (counting from sutural margin) and with one shortened vein, reaching basal one-third of elytron, between second and third veins. Scutellar groove not pronounced as separate groove.

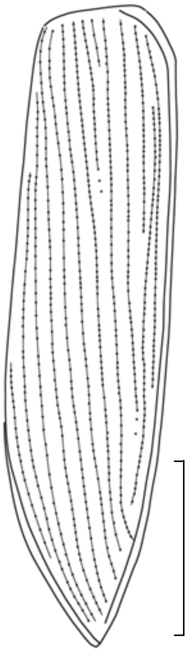


Fig. 29. *Sakmaracoleus orenburgensis* sp. nov., holotype PIN, no. 5273/3, elytron; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage. Scale bar, 1 mm.

Species composition. Type species.

Comparison. The new species strongly differs from all other Permian members of the family in the elongate parallel-sided elytron and shortened grooves at its base. Among previously described Triassic species, it is especially similar to the elytron of *Ulomites* Dunstan, 1924, described from the Upper Triassic of Australia in the family Tenebrionidae (without sufficiently justifying this systematic position), but the new species differs from it in the presence of shortened grooves at the elytral base. Such grooves are known in the Jurassic *Prostecogmus* Ponomarenko, 1986, but it has a totally different body shape.

Sakmaracoleus orenburgensis Ponomarenko, sp. nov.

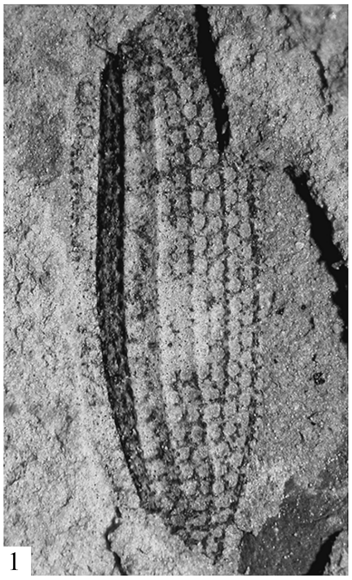
Plate 1, fig. 9.

Etymology. From the Orenburg Region.

Holotype. PIN, no. 5273/3, part and counterpart of left elytron; Kul'chumovo locality; Upper Permian, Vyatkian Stage.

Description (Fig. 29). The elytral base is straight, its apex is acute, symmetrical; the elytron is more than four times as long as wide; its sutural and

Plate 1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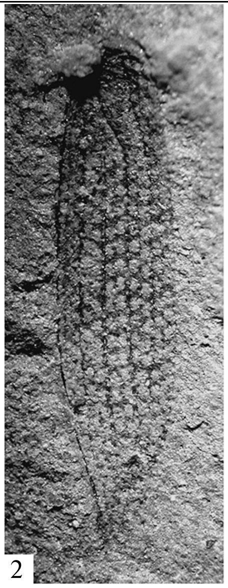
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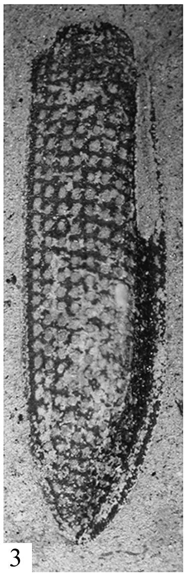
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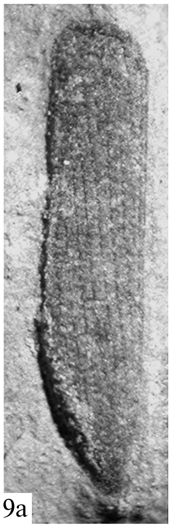
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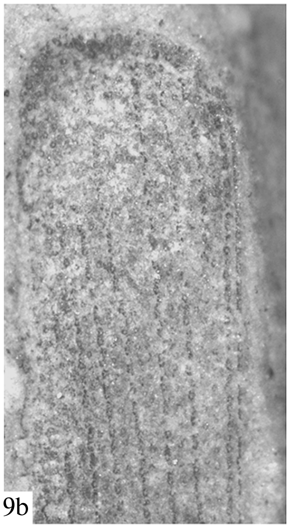
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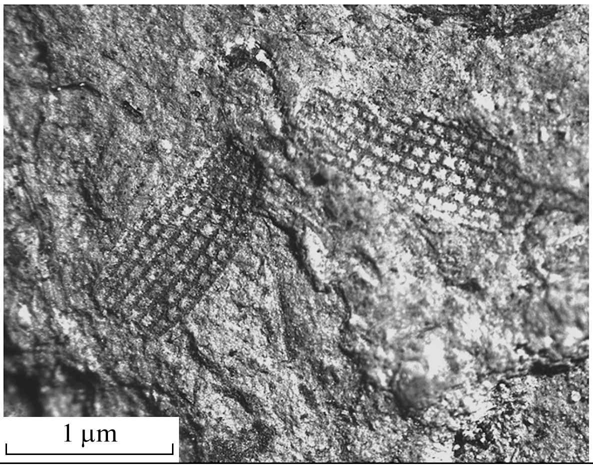
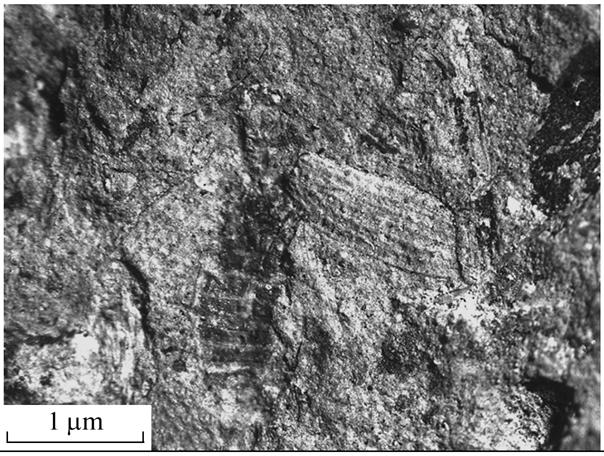




external margins are almost straight, bordered. The epipleural rim is wide. Of two shortened grooves, the anterior one is almost four times as long as the posterior groove. There are two closely set grooves near the sutural margin; the groove positioned closer to the suture extends slightly beyond the middle of the elytron; the other groove reaches the apical quarter of the elytron. Next to it, there is a shortened groove, which reaches only the basal one-third of the elytron. Punctures in the grooves are relatively small, rounded, arranged irregularly in the grooves; the distance between them is much greater than their diameter.

Measurements, mm. Elytral length, about 3.8; elytral width, 1.7.

Remarks. The elytron is crumpled in its basal half, so that the external margin of the elytral disc overlaps the external margin of the elytron and hides it. The marginal grooves and epipleural rim are not visible here.

Material. Holotype.

Family Asiocoleidae Rohdendorf, 1961

= Tricoleidae Ponomarenko, 1969, syn. nov.

Recently described beetles display a considerable diversity of venation, so that the gap between the families Asiocoleidae Rohdendorf, 1961 and Tricoleidae Ponomarenko, 1969 is insufficient to treat them as separate families. The family Tricoleidae Ponomarenko, 1969 should be regarded as a junior subjective synonym of Asiocoleidae Rohdendorf, 1961.

Genus *Bicoleus* Ponomarenko, gen. nov.

Etymology. From the Latin *bi-* (two) and the latinized Greek *koleos* (scale).

Type species. *Bicoleus kuplensis* sp. nov.

Diagnosis. Elytron convex, with two main veins and three fields between them. Epipleural rim rather wide, with one row of large cells. Main veins riblike, clearly distinguished from intermediate veins, and reaching external margin of elytron near elytral apex. External field wide, with five or six rows of cells in middle part of elytron; other fields in middle part of elytron with three or four rows of cells; base of elytron with up to eight rows of cells. Cells rounded, somewhat wider than veins. Tubercles bordering cells distinct.

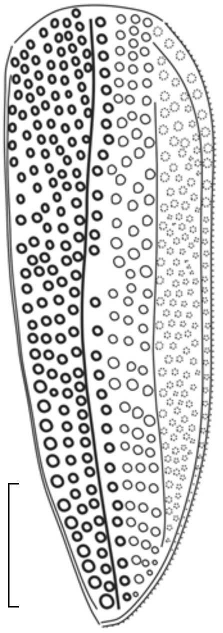


Fig. 30. *Bicoleus kuplensis* sp. nov., holotype PIN, no. 3700/188, elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage. Scale bar, 1 mm.

Species composition. Two new species described below.

Comparison. The new genus differs from the other genera of the family only in the two preserved main veins.

Bicoleus kuplensis Ponomarenko, sp. nov.

Plate 2, fig. 1

Etymology. From the Kuplya River.

Holotype. PIN, no. 3700/188, incomplete right elytron, Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Description (Fig. 30). The elytron is elongate, more than three times as long as wide, narrowed almost from the base; its apex is symmetrical; the sutural margin is almost straight, bordered. Each row contains about 30 cells; the cells are rounded square.

Explanation of Plate 1

Fig. 1. *Permocupes latus* sp. nov., holotype PIN, no. 3286/46, × 18.9; Chepanikha locality, Udmurtia; Urzhumian Stage.

Fig. 2. *Protocupoides elongatus* sp. nov., holotype PIN, no. 3286/45, × 17.4; Chepanikha locality, Udmurtia; Urzhumian Stage.

Fig. 3. *Protocupoides esini* sp. nov., holotype PIN, no. 3840/28, × 12.0; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 4. *Tecticupes martynovi* sp. nov., holotype PIN, no. 199/158a, × 17.8; Kargala locality, Orenburg Region; Urzhumian Stage.

Figs. 5 and 6. *Taldycupes cellulosus* sp. nov.; Isady locality, Vologda Region; Severodvinian Stage: (5) holotype PIN, no. 3840/438, × 16.9; (6) paratype PIN, no. 3840/437.

Figs. 7 and 8. *Simmondsia permiana* sp. nov.; Isady locality, Vologda Region; Severodvinian Stage: (7) holotype PIN, no. 3840/1602; (8) paratype PIN, no. 3840/688, part and counterpart.

Fig. 9. *Sakmaracoleus orenburgensis* sp. nov., holotype PIN, no. 5273/3; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage: (a) habitus, × 17.1; (b) elytral base, × 44.7; .

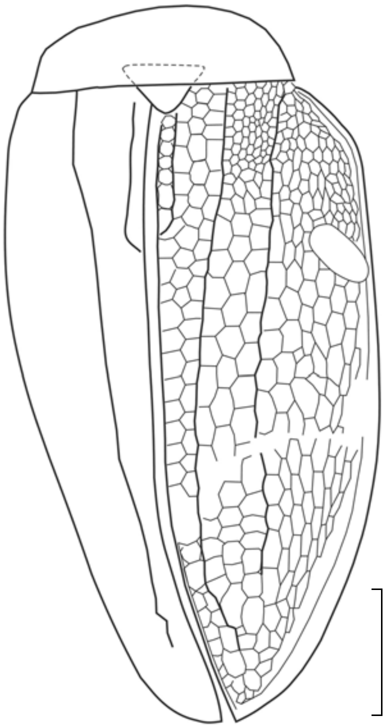


Fig. 31. *Bicoleus laticella* sp. nov., holotype PIN, no. 3840/1203, habitus; Isady locality, Vologda Region; Severodvinian Stage. Scale bar, 1 mm.

All main veins are free. The external field has six rows of cells; the next field has four rows of cells almost over its entire length; the field closest to the suture has three rows in the distal half; it is strongly dilated at the base, where it has six or seven rows of cells. The middle field is only slightly dilated at the base.

Measurements, mm. Elytral length, about 5; elytral width, 1.7.

Comparison. The new species is distinguished by the strongly basally dilated field closest to the suture.

Material. Holotype.

Bicoleus laticella Ponomarenko, sp. nov.

Plate 2, figs. 2 and 3

Etymology. From the Latin *latus* (wide) and *cella* (cell).

Holotype. PIN, no. 3840/1203, part and counterpart of pronotum and elytra; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 31). A medium-sized beetle. The elytron is flattened, wide, three times as long as wide, sharply dilated from the base, then, gradually narrowed almost to the apex; the elytral apex is asymmetrical, shifted towards the sutural margin; the sutural margin is straight up to its distal one-forth. Cells are large, longitudinally elongate, hexagonal, rarely almost oval, much wider than the veins; each row contains about 25 cells. The external field is very wide, not narrower than the other two fields taken together, and has more than six rows of cells. The middle field has three rows of cells over most of its length; basally, it has up to seven rows of small cells. The field closest to the suture has three rows of cells in its basal quarter and two rows of cells more distally. There are seven cells behind 3A.

Measurements, mm. Elytral length, 5.6; elytral width, 2.1.

Comparison. The new species differs from the type species in the very wide external field and in the narrowed other fields.

Material. In addition to the holotype, paratype PIN, no. 3840/398: incomplete elytron from the same locality.

Genus *Tetracoleus* Ponomarenko, 2009

The genus was described from the Triassic of the northern Cis-Ural Region. In the Upper Vyatkian Aristovo locality, an incomplete fossil elytron has been found, the preserved features of which do not contradict the assignment to this genus. Judging from the photograph provided by G. Beattie, a similar elytron was found in the Late Permian Newcastle Series of Australia. It probably belongs to a separate species, other than that from Aristovo.

Type species. *Tetracoleus tshalyshevi* Ponomarenko, 2009.

Explanation of Plate 2

Fig. 1. *Bicoleus kuplensis* sp. nov. holotype PIN, no. 3700/188, × 18.1; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Figs. 2 and 3. *Bicoleus laticella* sp. nov.; Isady locality, Vologda Region; Severodvinian Stage: (2) holotype PIN, no. 3840/1203: (2a, 2b) photographs of counter impression, with different illumination; (c) direct impression, × 12.9; (3) paratype PIN, no. 3840/398, × 12.

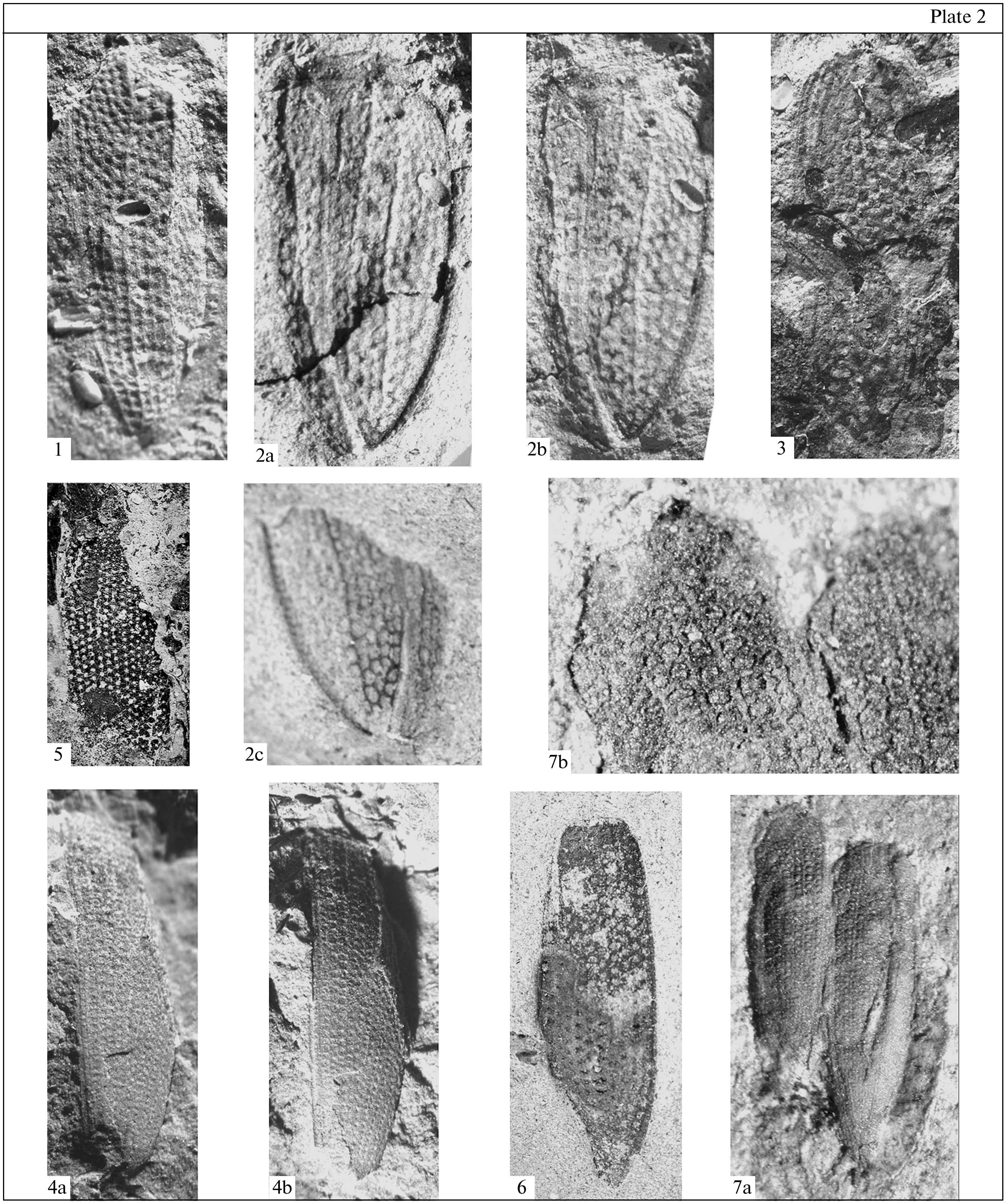
Fig. 4. *Tetracoleus orenburgensis* sp. nov., holotype PIN, no. 3700/189, × 15; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage: (4a, 4b) photographs, with different illumination.

Fig. 5. *Tetracoleus meyeni* sp. nov. holotype PIN, no. 3446/27, × 16.2; Aristovo locality, Vologda Region; Vyatkian Stage.

Fig. 6. *Tetracoleus tricoleoides* sp. nov., holotype PIN, 3840/1202, × 10.2; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 7. *Schizotaldycupes pubescens* sp. nov., holotype PIN, no. 3695/10: (7a) habitus, × 10; (7b) elytral base, × 36; Kostovaty locality, Udmurtia; Urzhumian Stage.

Plate 2



D i a g n o s i s. Elytron convex, with three main veins and four fields between them. Three main veins only slightly differing from intermediate veins. Marginal veins reaching elytral apex; other veins fused near apex. Elytral fields with three or four rows of cells in medial part; base of second field (counting from elytral margin) with up to eight rows of cells; base of field closest to suture with four rows of cells. Cells rounded,

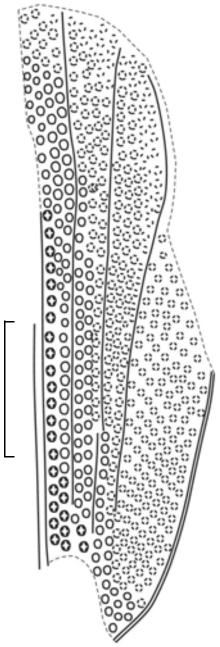


Fig. 32. *Tetracoleus orenburgensis* sp. nov., holotype PIN, no. 3700/189, elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage. Scale bar, 1 mm.

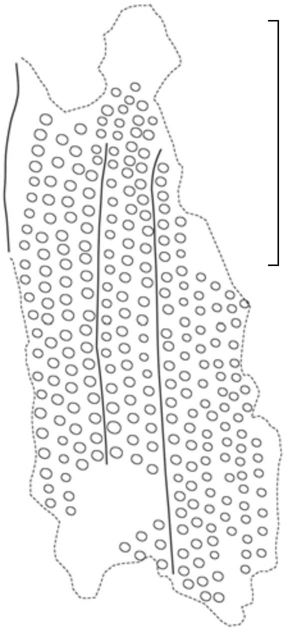


Fig. 33. *Tetracoleus meyeni* sp. nov., holotype PIN, no. 3446/27, elytron; Aristovo locality, Vologda Region; Vyatkian Stage. Scale bar, 1 mm.

significantly wider than veins. Tubercles bordering cells distinct.

Species composition. Two species from the Middle Triassic of the northern Ural Mountains and two species described below from the terminal Permian.

Comparison. The genus differs from other genera in the four rows of cells in the field closest to the margin and the second field from the suture and in the greater number of rows at the base of the other fields.

Tetracoleus orenburgensis Ponomarenko, sp. nov.

Plate 2, fig. 4

Etymology. From the city of Orenburg.

Holotype. PIN, no. 3700/189, incomplete right elytron, Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Description (Fig. 32). The elytron is elongate, almost four times as long as wide, narrowed almost from the base; its apex is shifted towards the sutural margin; the sutural margin is almost straight, bordered. The epipleural rim is narrow. Each row contains about 40 cells; the cells are rounded square. All of main veins are free. Distally, the external field contains five rows of cells; the next field has four rows of cells and is narrowed posteriad, so that the rows of cells start wedging out in its middle part; the field closest to the suture has three rows of cells and is dilated basally, where it has six rows of cells. The elytral cells do not form regular transverse rows.

Measurements, mm. Elytral length, about 4; elytral width, about 1.

Comparison. The new species is distinguished by the rows of cells wedging out in the middle field.

Material. Holotype.

Tetracoleus meyeni Ponomarenko, sp. nov.

Plate 2, fig. 5

Etymology. In memory of the eminent paleobotanist S.V. Meyen.

Holotype. PIN, no. 3446/27, middle part of elytron, flattened and preserved as carbonized film; Aristovo locality, Vologda Region; Upper Permian, Vyatkian Stage.

Description (Fig. 33). The elytron is wide, probably flattened. The epipleural rim is narrow. The cells are rounded. The subcostal and anal fields have four rows of cells each, almost over the entire length of the field; other fields have three rows. The main veins only slightly differ from the intermediate veins; the intermediate veins are straight, the third vein is oblique basally. The elytral cells alternate and do not form regular transverse rows.

Measurements, mm. Elytral length, about 4; elytral width, 1.

Comparison. Comparison is hindered by the incompleteness of the specimen. The new species is similar to *T. orenburgensis* sp. nov. described above and differs from it in the four rows of cells in the second field, counting from the suture.

Material. Holotype.

Tetracoleus tricoleoides Ponomarenko, sp. nov.

Plate 2, fig. 6

Etymology. From the generic name *Tricoleus*.

Holotype. PIN, no. 3840/1202, direct impression of left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 34). The elytron is rather wide, convex, 3.4 times as long as wide, dilated from the base to the middle, narrowed behind the middle, protruding as a "tail" near its apex; the apex is symmetrical; the sutural margin is almost straight, bordered; the elytral base is straight. The epipleural rim is narrow. Each row contains about 30 cells; the cells are rounded. All ribs at the main veins are shortened, free; the second rib from the external margin is very poorly pronounced. The external field has three rows of cells up to its middle; more distally, it has two rows of cells; the next field has three rows of cells; the next, two rows; the field closest to the suture and preceding field are dilated basally, where they have up to five rows of small cells. The elytral cells are rounded, somewhat wider than the spaces between them, and do not form regular transverse rows.

Measurements, mm. Elytral length, 6; elytral width, 2.

Comparison. The new species is distinguished by the rather wide elytron, dilated medially and having the apex protruding as a tail, and by the shortened ribs of the main veins.

Remarks. The shape of the elytron and rounded cells make the new species similar to Triassic members of the genus *Tricoleus*, from which it differs in the number of cell rows in most of the fields.

Material. Holotype and paratype PIN, no. 3840/1275, apex of elytron from the same locality.

Genus *Schizotaldycupes* Rohdendorf, 1961

The genus was originally described in the family Taldycupedidae (Rohdendorf, 1961) and, then, transferred to the family Rhombocoleidae because of the specific venation and presence of a *schiza* (Ponomarenko, 1969). Now, in the light of finding Permian asiocoleids similar to this genus in venation, it is expedient to transfer it to the family Asiocoleidae. The elytral cells of *Schizotaldycupes* are bordered by characteristic tubercles, as in other tricoleids. The presence of a schiza should not be regarded as a strong argument against this transfer, because this kind of lock has been recorded in the elytra of beetles from many different families.

The beetle described below at first glance seems to be a typical higher schizophoroid, with the cells transformed into internal columellae; however, electron microscopy shows that these are external cells, bordered by tubercles bearing hairs (Fig. 15a). It is likely that similar changes also took place in the course of fossilization of the beetle described below as *S. angustior*.

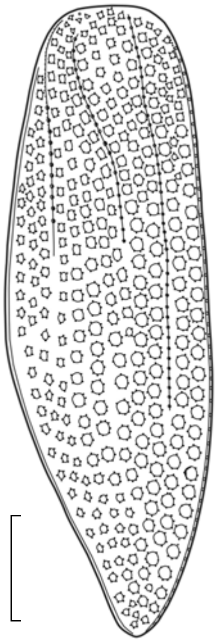


Fig. 34. *Tetracoleus tricoleoides* sp. nov., holotype PIN, 3840/1202, elytron; Isady locality; Upper Permian, Severodvinian Stage. Scale bar, 1 mm.

Schizotaldycupes pubescens Ponomarenko, sp. nov.

Plate 2, fig. 7

Etymology. From the Latin *pubescens* (hairy).

Holotype. PIN, no. 3695/10, paired elytra and abdomen, widely separated, but undoubtedly belonging to the same specimen; Kostovaty locality, Udmurtia; Urzhumian Stage.

Description (Fig. 35). The elytron is elongate, convex, widest in front of the middle, and gradually narrowing towards its apex. The elytral base is convex; its external margin is evenly convex; its sutural margin is almost straight in the basal half. The epipleural rim is narrow; the sutural rim is wide, with a row of cells. The main veins are much narrower than cells. The cells are rounded; each row contains about 40 cells. The subcostal (external) field has at least four rows of cells. The next field and the field closest to the suture have two rows of cells each, almost over their entire length; the field between them has three rows of cells, but basally it has at least six rows of cells. The main veins only slightly differ from the intermediate veins; the intermediate veins are straight, the basal part of the third vein is oblique. The elytral cells alternate and do

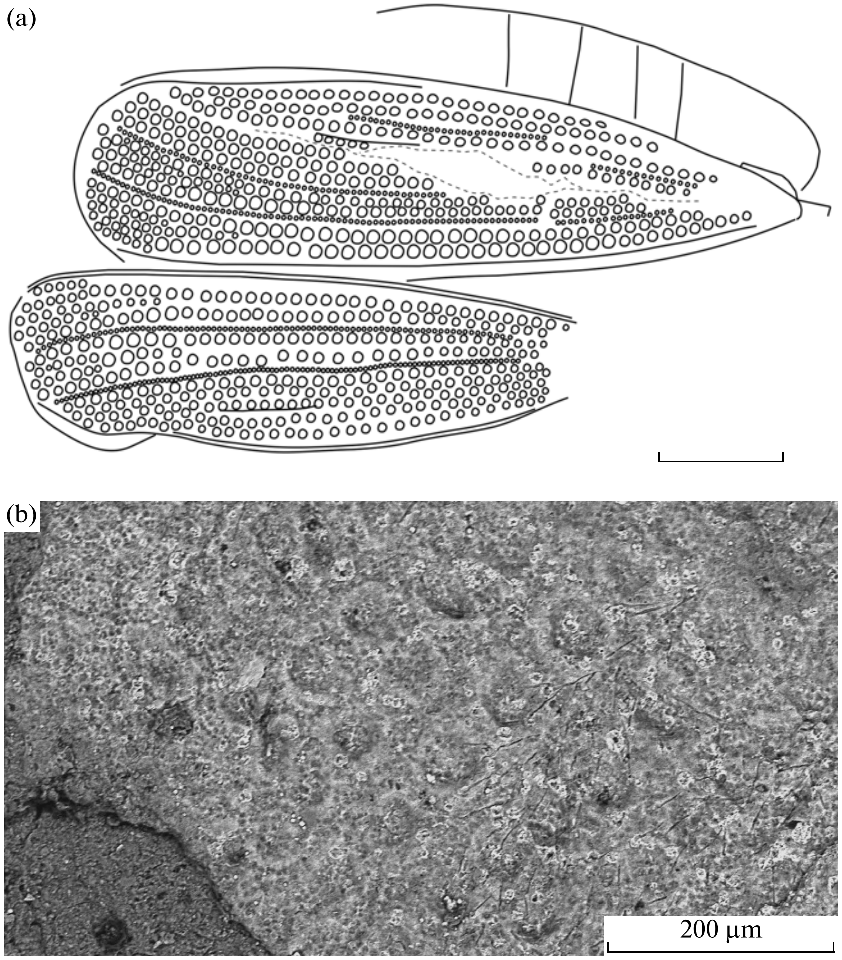


Fig. 35. *Schizotaldycupes pubescens* sp. nov., holotype PIN, no. 3695/10; Kostovaty locality, Udmurtia; Urzhumian Stage: (a) habitus; (b) SEM image of elytron fragment;. Scale bar in (a), 1 mm.

not form regular transverse rows. The main veins are much narrower than cells.

Measurements, mm. Elytral length, 5.8; elytral width, 1.8.

Comparison. The new species is distinguished by the more acute elytral apex, fewer cells in two fields closest to the external margin, and the greater number of cells in the next field.

Material. Holotype.

Family Rhombocoleidae Rohdendorf, 1961

Genus *Rhombocoleus* Rohdendorf, 1961

The new species described below is assigned to the genus *Rhombocoleus* because of its compliance with the diagnosis of this genus: relatively narrow elytron with almost straight external and sutural margins and five rows of large punctures in external elytral field.

Rhombocoleus gomankovi Ponomarenko, sp. nov.

Plate 3, fig. 1

Etymology. In honor of the distinguished paleobotanist A.V. Gomankov.

Holotype. PIN, no. 3700/191, incomplete direct impression of elytron; Novo-Aleksandrovka locality; Upper Permian, Severodvinian Stage.

Description (Fig. 36). The elytron is elongate, only slightly dilated from the base; its external and internal margins are straight and almost parallel; the base is rounded; the sutural margin is bordered. The epipleural rim is narrow. The schiza is short, located in the proximal one-third of the elytron near its sutural margin. The elytral surface is densely and finely punctate. The elytral ribs are hardly discernible, not curved towards the external margin near the base. The grooves are poorly visible; punctures in the grooves are large. The external field has five rows of poorly visible punctures; the other fields have three such rows each; basally, the punctures are smaller, and additional rows of punctures are present.

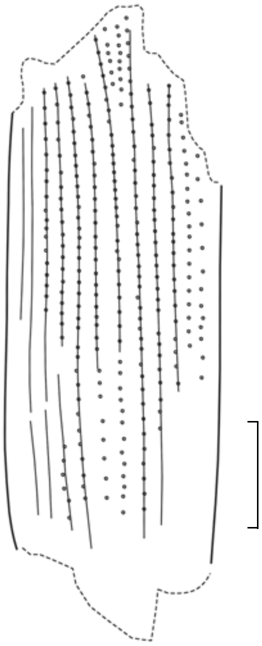


Fig. 36. *Rhombocoleus gomankovi* sp. nov., holotype PIN, no. 3700/191, elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage. Scale bar in Figs. 36–59, 1 mm.

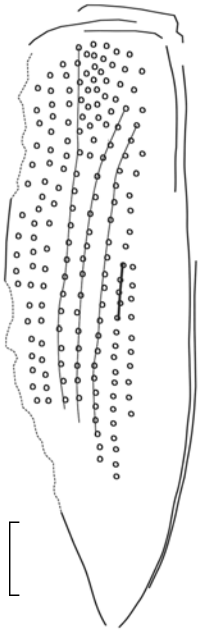


Fig. 37. *Karakanocoleus mutovinensis* sp. nov., holotype PIN, no. 3840/439, elytron; Isady locality, Vologda Region; Severodvinian Stage.

Measurements, mm. Length of preserved part of elytron, 6.2; total elytral length, about 10; elytral width, 1.9.

Comparison. The new species differs from congeners in the larger and wider elytron, almost straight elytral ribs, and the larger punctures in the rows.

Material. Holotype.

Genus *Karakanocoleus* Rohdendorf, 1961

Karakanocoleus mutovinensis Ponomarenko, sp. nov.

Plate 3, fig. 2

Etymology. From Mutovino, an alternative name of the Isady locality.

Holotype. PIN, no. 3840/439, right elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 37). The elytron is slightly convex, approximately three times as long as wide; its base is wide; its basal two-thirds are dilated only slightly distally, so that the elytron was weakly convex; the elytron is narrowed in its apical one-third; its apex is acute; the sutural margin is almost straight, bordered. The epipleural rim is weakly dilated in the basal on-third of the elytron, becoming narrow in the distal part. The schiza is one-tenth of the elytron length, located proximal to the middle of the elytron, approximately at one-third of its width. The elytron surface has large, rather shallow impressions in grooves, especially distinct in the half of the elytron closest to the suture. The puncture grooves join the marginal groove, which runs along the sutural margin.

Measurements, mm. Elytral length, 4.0–4.5; elytral width, 1.0–1.3.

Comparison. The new species differs from congeners in the closest to the suture grooves joining the marginal groove, instead of running parallel to the sutural margin of the elytron.

Material. Holotype.

Genus *Erunakicupes* Rohdendorf, 1961

Erunakicupes grossus Ponomarenko, sp. nov.

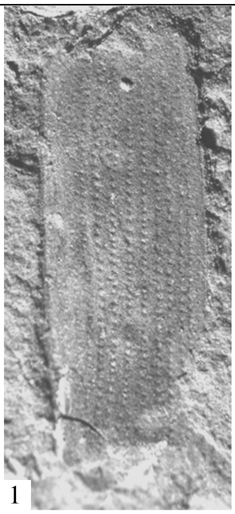
Plate 3, fig. 3

Etymology. The Latin *grossus* (huge).

Holotype. PIN, no. 3840/440, left elytron; Isady locality; Upper Permian, Severodvinian Stage.

Description (Fig. 38). The elytron is very weakly convex, three times as long as wide; its base is wide, oblique; its basal two-thirds are dilated only slightly distally, so that the elytron was weakly convex; the elytron narrows in its apical one-third; its apex is acute, slightly asymmetric, shifted towards the sutural margin; the sutural margin is almost straight, bordered. The epipleural rim is narrow. The schiza is one-tenth as long as the elytron, located proximal to the middle of the elytron, approximately at a quarter of its width. Additional puncture grooves in the basal part of the elytron are very short, include only a few punctures, and come only slightly onto the elytral disc.

Plate 3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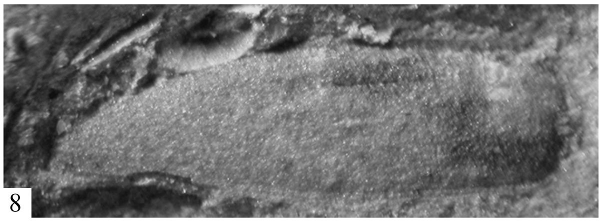
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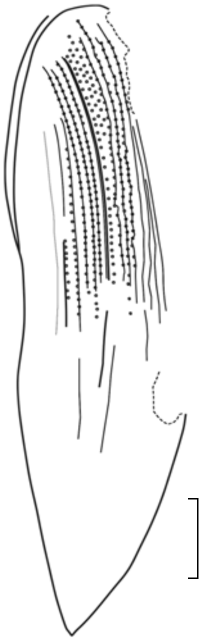


Fig. 38. *Erunakicupes grossus* sp. nov., holotype PIN, no. 3840/440, elytron; Isady locality, Vologda Region; Severodvinian Stage.

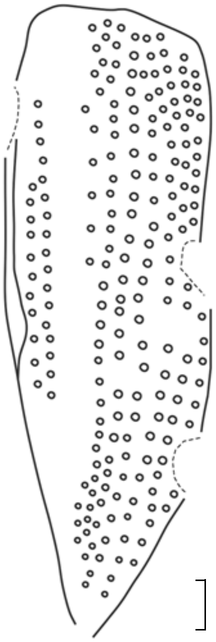


Fig. 39. *Aenigmocoleus uralensis* sp. nov., holotype PIN, no. 5273/4, elytron; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

Puncture grooves in the sutural area are parallel to the sutural margin.

Measurements, mm. Elytral length, 2.1–2.3; elytral width, 0.7–0.9.

Comparison. The new species differs from congeners in the short additional grooves in the basal part of the elytron.

Material. Holotype.

Genus *Aenigmocoleus* Rohdendorf, 1961

The new species described below is assigned to the genus *Aenigmocoleus* because of its compliance with the diagnosis of this genus: rather narrow elytron with almost straight external margin and strongly convex sutural margin, short groove, and longitudinal rows of widely spaced punctures.

Aenigmocoleus uralensis Ponomarenko, sp. nov.

Plate 3, fig. 4

Etymology. From the Urals.

Holotype. PIN, no. 5273/4, counter impression of right elytron; Kul'chumovo locality; Upper Permian, ?Vyatkian Stage.

Description (Fig. 39). The elytron is elongate, narrowing in its apical one-third, almost three times as long as wide; its base is rounded; its sutural margin is almost straight in the basal two-thirds and curved very weakly distally; the elytral apex is acute, asymmetrically shifted towards the sutural margin; the sutural margin is bordered, curved almost from the base, so that the elytron was strongly convex. The epipleural rim is dilated in the basal and apical thirds of the elytron. The schiza is one-fifth as long as the elytron, located in the proximal one-third of the elytron near

Explanation of Plate 3

Fig. 1. *Rhombocoleus gomankovi* sp. nov., holotype PIN, no. 3700/191, × 14.6; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Fig. 2. *Karakanocoleus mutovinensis* sp. nov., holotype PIN, no. 3840/439, × 16.6; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 3. *Erunakicupes grossus* sp. nov., holotype PIN, no. 3840/440, × 14.6; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 4. *Aenigmocoleus uralensis* sp. nov., holotype PIN, no. 5273/4, × 5.1; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

Fig. 5. *Rossocoleus angustus* sp. nov., holotype PIN, no. 3286/47, × 17; Chepanikha locality, Udmurtia; Urzhumian Stage.

Fig. 6. *Rossocoleus novojilovi* sp. nov., holotype PIN, no. 3286/48, × 20; Chepanikha locality, Udmurtia; Urzhumian Stage.

Fig. 7. *Rossocoleus aristovi* sp. nov., holotype PIN, no. 3840/1274, × 14; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 8. *Rossocoleus sakmara* sp. nov., holotype PIN, no. 5273/2, × 4.8; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

Fig. 9. ?*Rossocoleus sakmara* sp. nov., specimen PIN, no. 5273/5, × 6.5; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

Fig. 10. *Rhombocoleites uralensis* sp. nov., holotype PIN, no. 2695/11, × 23.2; Kostovaty locality, Udmurtia; Urzhumian Stage.

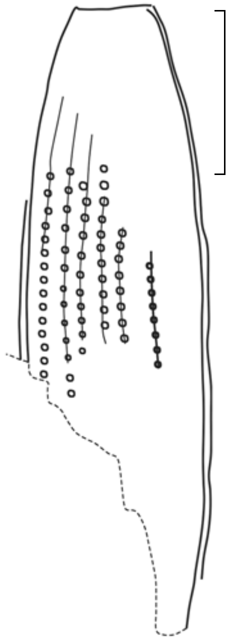


Fig. 40. *Rossocoleus angustus* sp. nov., holotype PIN, no. 3286/47, elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

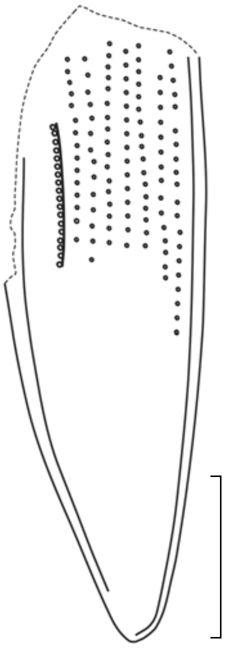


Fig. 41. *Rossocoleus novojilovi* sp. nov., holotype PIN, no. 3286/48, elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

the sutural margin. The surface of the elytron is covered with small tubercles and has eight rows of large widely spaced punctures; the spaces between them are several times as great as the puncture diameter. In some areas, the punctures are located in hardly visible grooves.

Measurements, mm. Elytral length, 10.0; elytral width, 3.3.

Comparison. The new species differs from congeners in the larger and wider elytron and larger punctures in the rows.

Material. Holotype.

Genus *Rossocoleus* Rohdendorf, 1961

Rossocoleus angustus Ponomarenko, sp. nov.

Plate 3, fig. 5

Etymology. From the Latin *angustus* (narrow).

Holotype. PIN, no. 3286/47, direct impression of incomplete right elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Fig. 40). The elytron is probably symmetrical, narrow, more than four times as long as wide; its base is narrow, straight; the elytron is dilated from the base to its basal quarter, narrowing behind the middle, bordered. The sutural margin is strongly convex, so that the elytral apex was certainly symmetrical. The epipleural rim is narrow. The schiza is one-fifth as long as the elytron, located proximal to the middle of the elytron, almost in the middle of its width. The elytron surface has longitudinal impressions in the sutural area.

Measurements, mm. Elytral length, more than 4; elytral width, 1.

Comparison. The new species differs from congeners in the narrow symmetrical elytron, narrow base, and almost symmetrical location of the schiza.

Material. Holotype.

Rossocoleus novojilovi Ponomarenko, sp. nov.

Plate 3, fig. 6

Etymology. In memory of the distinguished paleontologist N.I. Novozhilov, who was the first to find fossil insects in the Chepanikha locality.

Holotype. PIN, no. 3286/48, direct impression of left elytron; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Fig. 41). The elytron is asymmetrical, rather wide, 3.4 times as long as wide; its base is wide, oblique; the elytron is weakly dilated directly behind the base, narrowing distally; the elytral apex is blunt; the sutural margin is almost straight, bordered. The epipleural rim is narrow. The schiza is one-fourth as long as the elytron, located proximal to the middle of the elytron, near its external margin. The surface of the elytron has rows of large, rather shallow impressions, especially distinct in the sutural area.

Measurements, mm. Elytral length, 4.0; elytral width, 1.3.

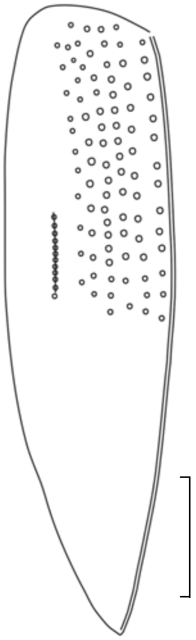


Fig. 42. *Rossocoleus aristovi* sp. nov., holotype PIN, no. 3840/1274, elytron; Isady locality, Vologda Region; Severodvinian Stage.

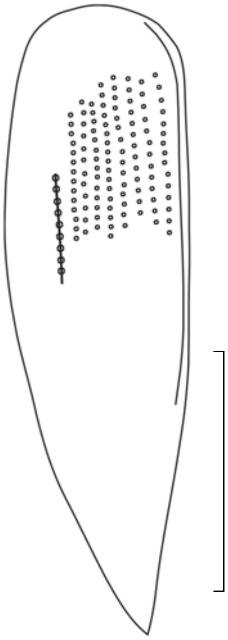


Fig. 43. *Rossocoleus sakmara* sp. nov., holotype PIN, no. 5273/2, elytron; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

Comparison. The new species differs from congeners in the larger, asymmetric elytron and from most of them in the long schiza located near the external margin. It differs from large *R. altus* Ponomarenko in the elytron dilated behind the middle, i.e., convex in living beetles.

Material. Holotype.

Rossocoleus aristovi Ponomarenko, sp. nov.

Plate 3, fig. 7

Etymology. In honor of the paleoentomologist D.S. Aristov.

Holotype. PIN, no. 3840/1274, left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 42). The elytron is medium-sized, slightly asymmetrical; its apex is shifted somewhat towards the external margin; the elytron is 3.4 times as long as wide; its base is narrow, rounded, slightly more than one-third as wide as the elytron in the middle; the elytron is dilated directly behind the middle, narrowing distal to the middle; its apex is acute; the sutural margin is more strongly convex than the external margin, bordered. The external margin is very weakly convex. The epipleural rim is narrow. The schiza is one-sixth as long as the elytron, located proximal to the middle of the elytron, near its external margin. The elytron surface has rows of large, rather shallow impressions, especially pronounced in the basal half.

Measurements, mm. Elytral length, 5.0; elytral width, 1.5.

Comparison. The new species differs from all congeners in the narrow elytral base.

Material. Holotype.

Rossocoleus sakmara Ponomarenko, sp. nov.

Plate 3, fig. 8

Etymology. From the Sakmara River.

Holotype. PIN, no. 5273/2, direct impression of right elytron; Kul'chumovo locality, Orenburg Region; Upper Permian, ?Vyatkian Stage.

Description (Fig. 43). The elytron is asymmetrical, rather wide, 3.3 times as long as wide; its base is not wide, straight, dilated noticeably medially, narrowing distally, where the outline of the elytron is rounded convex; the elytral apex is blunt; the sutural margin is bordered, very weakly convex. The schiza is one-fourth as long as the elytron, located proximal to the middle of the elytron, near its external margin. The elytron surface has rows of large, rather shallow impressions.

Measurements, mm. Elytral length, 2.3; elytral width, 0.7.

Comparison. The new species is very similar to *R. novojilovi* and differs from it in the smaller elytron, dilated towards the middle, distally, with a rounded convex external margin more.

Material. Holotype.

Fig. 44. *?Rossocoleus sakmara* sp. nov., specimen PIN, no. 5273/5, habitus; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

The same locality has yielded a relatively completely preserved fossil beetle (specimen PIN, no. 5273/5), the elytral morphology of which is indiscernible. Judging from the body size and shape, the elytron described above could belong to the same species; the two specimens probably represent the same dismembered beetle. Therefore, the description of the latter fossil given below is provisionally assigned to the same species, although it has not been included in the type series. The specimen consists of a metaventrite, four basal ventrites of the abdomen, and isolated and turned for 90° head and pronotum lying in front of the metaventrite. This specimen differs from all other fossil beetle bodies described in the formal genus *Rhombocoleites* in the shape of the metaventrite, which is trapezoid rather than rounded narrowing anteriad.

Description (Fig. 44; Pl. 3, fig. 9). A relatively small, elongate oval, flattened beetle. The metaventrite is transverse, but rather long, strongly narrowing anteriad, 1.8 times as long as wide at the posterior margin, with straight lateral margins. The paracoxal and trochantinal sutures are distinct. The metepisternum reaches the mesocoxal cavity and is strongly, but gradually anteriorly dilated; its anterior margin is three times as wide as the posterior margin. The metacoxae completely separate the metaventrite and abdomen and are much wider than long. Four preserved basal abdominal ventrites are subequal in length. The schiza is long, located at the very base of the abdomen; the epipleural rim is narrow. The entire body is covered with small dense tubercles.

Measurements, mm. Body length, about 4; body width, 1.6; elytral length, 3.7.

Genus *Rhombocoleites* Ponomarenko, 1969

Rhombocoleites uralensis Ponomarenko, sp. nov.

Plate 3, fig. 10

Etymology. From the Urals.

Holotype. PIN, no. 3695/11, part and counterpart of beetle without head, prosternum, and legs; Kostovaty locality, Udmurtia; Urzhumian Stage.

Description (Fig. 45). A rather small, elongate oval, flattened beetle. The mesoventrite is short, 2.5 as wide as long, shorter than the mesocoxa. The mesepimeron is smaller than the mesepisternum; together they form an almost regular rectangle. The mesocoxa is longer than wide. The metaventrite is transverse, occupies most of the metathorax, 2.6 times wider than long at the posterior margin; its lateral margins are very weakly rounded. The metepisterna reach the mesocoxal cavity and are strongly, but gradually anteriorly dilated; the anterior margin is thrice as wide as the posterior margin. The metacoxae completely separate the metaventrite and abdomen and are much wider than long. The elytra are narrow, 4.5 times as long as wide, narrowing in the apical part. The schiza (possibly, it is a protuberance on the paratergites) is long, running from the base of the abdomen to the middle of the second abdominal ventrite. The entire body is covered with small dense tubercles.

Measurements, mm. Body length, about 4; body width, 1.6; elytral length, 3.7.

Comparison. The new species is distinguished by the narrowed, less wide metaventrite.

Material. Holotype.

Family Schizocoleidae Rohdendorf, 1961

Genus *Schizocoleus* Rohdendorf, 1961

The species described below are assigned to the genus *Schizocoleus* because of their compliance with its diagnosis: elytron weakly convex, with almost parallel margins in basal half.

Schizocoleus longus Ponomarenko, 2004

Plate 4, fig. 1

Schizocoleus longus: Ponomarenko, 2004, p. 194, pl. 2, fig. 5.

Etymology. The Latin *longus* (long).

Holotype. PIN, no. 3700/41, incomplete part and counterpart of elytra; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Redescription (Fig. 46). The elytron is convex, elongate, more than four times as long as wide; its base is wide, with the basal two-thirds dilated only slightly distally; the elytron narrows in the apical one-third; its apex is acute; the sutural margin is weakly

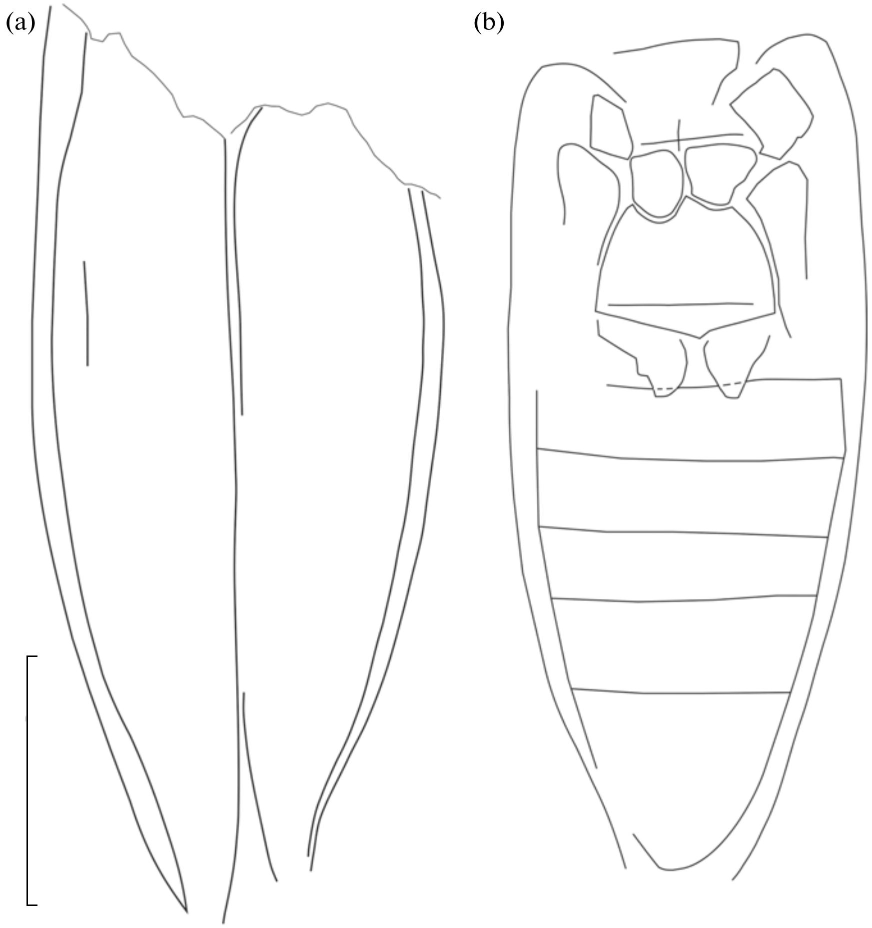


Fig. 45. *Rhombocoleites uralensis* sp. nov., holotype PIN, no. 2695/1, habitus; Kostovaty locality, Udmurtia; Urzhumian Stage: (a) dorsal and (b) ventral views.

convex, bordered. The epipleural rim is narrow. The schiza is one-fifth as long as the elytron, located proximal to the middle of the elytron, approximately at one-fourth of its length. The elytron surface is covered with small dense tubercles.

Measurements, mm. Holotype: length of preserved part of elytron, 2.2. New specimen: elytral length. 6; elytral width, 1.6.

Comparison. The new species differs from congeners in the strongly elongate elytra.

Material. New specimen from the type locality, PIN, no. 3700/186, part and counterpart of left elytron, (Pl. 4, fig. 1).

Schizocoleus minimus Ponomarenko, sp. nov.

Plate 4, fig. 2

Etymology. The Latin *minimus* (smallest).

Holotype. PIN, no. 3700/190, incomplete direct impression of elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Description (Fig. 47). The elytron is small, convex; its base is wide and rounded, not bordered; the elytron is only slightly dilated from the base, parallel-sided, with the external margin without a notch; and the sutural margin is almost straight, bordered. The epipleural rim is narrow. The schiza is rather long, located proximal to the middle of elytra, close to one-fourth of its width. The elytron surface is covered with small closely spaced tubercles.

Measurements, mm. Length of preserved part of elytron, 1.8; estimated elytral length, 2.5; elytral width, 0.7.

Comparison. The smallest known member of the genus, distinguished by the rounded elytral base and almost parallel sides of the elytron.

Material. Holotype.

Schizocoleus robustus Ponomarenko, sp. nov.

Plate 4, fig. 3

Etymology. The Latin *robustus* (massive).

Holotype. PIN, no. 3700/192, incomplete direct impression of elytra; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Description (Fig. 48). The elytron is convex; its base is wide, slightly oblique, bordered; the elytron is dilated weakly distally before the proximal end of the

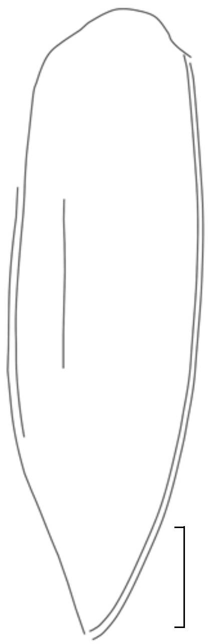


Fig. 46. *Schizocoleus longus* Ponomarenko, 2004, specimen PIN, no. 3700/186, elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

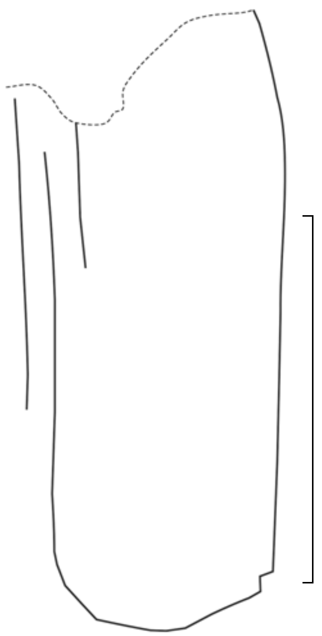


Fig. 47. *Schizocoleus minimus* sp. nov., holotype PIN, no. 3700/190, elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

schiza, with the external margin notched at the level of the schiza and weakly convex, bordered sutural margin. The epipleural rim is narrow. The schiza is rather short, located proximal to the middle of the elytron, close to one-fourth of its width. The elytron surface is covered with very small closely spaced tubercles.

Measurements, mm. Length of preserved part of elytron, 6.1; estimated elytral length, more than 10; elytral width, 2.7.

Comparison. One of the largest members of the genus, distinguished from *S. major* from the Kul'chumovo locality, described below, by the oblique elytral base and small punctation of the surface.

Material. Holotype.

Schizocoleus depressus Ponomarenko, sp. nov.

Plate 4, fig. 4

Etymology. From the Latin *depressus* (flattened).

Holotype. PIN, no. 3840/1278, incomplete direct impression of left elytron; Isady locality, Vologda Region; Severodvinian Stage.

→

Explanation of Plate 4

Fig. 1. *Schizocoleus longus* Ponomarenko, 2004, specimen PIN, no. 3700/186, × 10; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Fig. 2. *Schizocoleus minimus* sp. nov., holotype PIN, no. 3700/190, × 33; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Fig. 3. *Schizocoleus robustus* sp. nov., holotype PIN, no. 3700/192, × 8.4; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Fig. 4. *Schizocoleus depressus* sp. nov., holotype PIN, no. 3840/1278, × 18; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 5. *Schizocoleus major* sp. nov., holotype PIN, no. 5273/1, × 6.8; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

Fig. 6. *Uskatocoleus uralensis* sp. nov., holotype PIN, no. 5276/1, × 11.8; Babintsevo locality, Orenburg Region; Severodvinian Stage.

Fig. 7. *Uskatocoleus sukhonenis* sp. nov., holotype PIN, no. 3840/1273, × 6.8; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 8. *Uskatocoleus convexus* sp. nov., holotype PIN, no. 3840/1205, × 25.2; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 9. *Uskatocoleus micron* sp. nov., holotype PIN, no. 3840/417, × 26.8; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 10. *Pseudochrysomelites longus* sp. nov., holotype PIN, no. 3840/1208, × 37; Isady locality, Vologda Region; Severodvinian Stage.

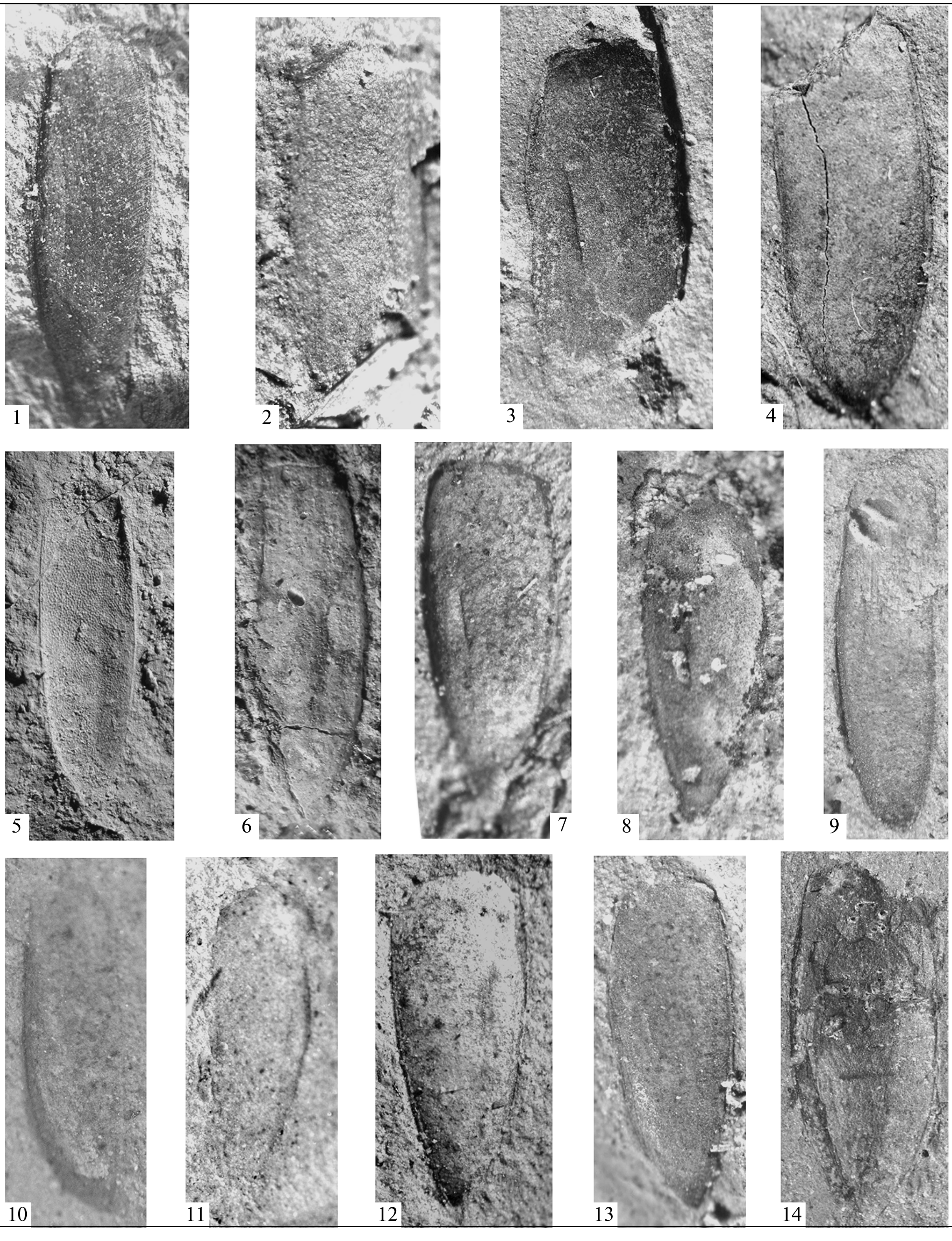
Fig. 11. *Pseudochrysomelites medialis* sp. nov., holotype PIN, no. 3840/1671, × 22.9; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 12. *Pseudochrysomelites sphenoidalis* sp. nov., holotype PIN, no. 3840/1268, × 22.1; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 13. *Pseudochrysomelites bashkuevi* sp. nov., holotype PIN, no. 3840/1276, × 20.3; Isady locality, Vologda Region; Severodvinian Stage.

Fig. 14. Schizophoridae incertae sedis, specimen PIN, no. 3286/142, habitus, × 16.2; Chepanikha locality, Udmurtia; Urzhumian Stage.

Plate 4



Description (Fig. 49). The elytron is convex; its base is wide, straight; the elytron is only slightly dilated from the base to the apical one-third, more distally, symmetrically rounded notched, with the external margin notched at the level of the schiza; the sutural margin is bordered. The elytron is 2.8 times as long as wide. The epipleural rim is narrow. The elytron surface is covered with very small closely spaced tubercles.

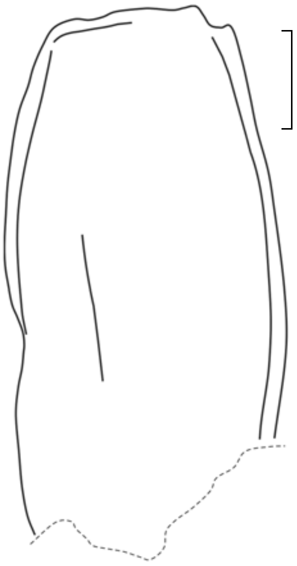


Fig. 48. *Schizocoleus robustus* sp. nov., holotype PIN, no. 3700/192, elytron; Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

Measurements, mm. Elytral length, about 5; elytral width, 1.8.

Comparison. A medium-sized member of the genus, especially similar in elytron shape and surface type to *S. major* sp. nov. and differing from it in the half as large size and the weaker notch in the external margin of the elytron.

Material. Holotype.

Schizocoleus major Ponomarenko, sp. nov.

Plate 4, fig. 5

Etymology. The Latin *major* (greater, larger).

Holotype. PIN, no. 5273/1, part and counterpart of elytron; Kul'chumovo locality, Orenburg Region; Upper Permian, ?Vyatkian Stage.

Description (Fig. 50). The elytron is weakly convex, 1.4 times longer than wide; its base is wide, straight, flattened; the basal three-fourths of the elytron are only slightly distally dilated; the elytron narrows in the apical quarter; the inflection of the external margin is somewhat distal to the inflection of the sutural margin; the apex is rounded; the sutural margin is almost straight, bordered, with a row of large punctures, with a distinct square notch for the scutellum near the base. The epipleural rim is narrow. The schiza is one-tenth of the elytron length, located proximal to the middle of the elytron, close to one-third of its width. The elytron surface is covered with large closely spaced tubercles.

Measurements, mm. Elytral length, 12.5; elytral width, 3.5.

Comparison. The new species differs from congeners in the larger size, more distal point where the elytron starts narrowing, the straight and not bordered elytron base, and the coarse punctation of the elytron.

Remarks. A similar elytral morphology, with large densely spaced tubercles, is found in the majority of members of the family Schizophoridae.

Material. Holotype.

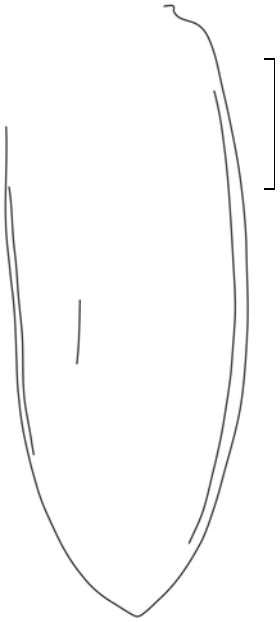


Fig. 49. *Schizocoleus depressus* sp. nov., holotype PIN, no. 3840/1278, elytron; Isady locality, Vologda Region; Severodvinian Stage.

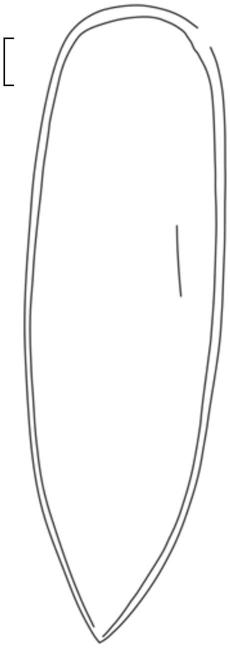


Fig. 50. *Schizocoleus major* sp. nov., holotype PIN, no. 5273/1, elytron; Kul'chumovo locality, Orenburg Region; ?Vyatkian Stage.

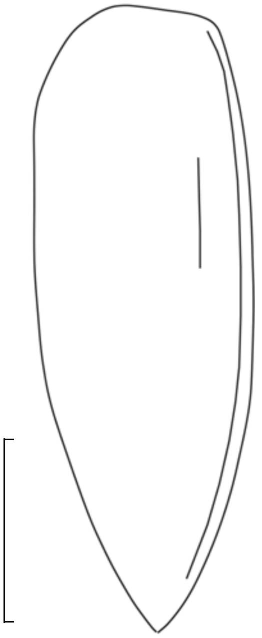


Fig. 51. *Uskatocoleus uralensis* sp. nov., holotype PIN, no. 5276/1, elytron; Babintsevo locality, Orenburg Region; Severodvinian Stage.

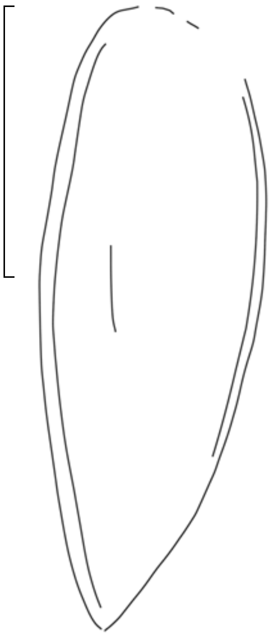


Fig. 52. *Uskatocoleus convexus* sp. nov., holotype PIN, no. 3840/1205, elytron; Isady locality, Vologda Region; Severodvinian Stage.

Genus *Uskatocoleus* Rohdendorf, 1961

The new species described below is assigned to the genus *Uskatocoleus* because of its compliance with the diagnosis of this genus: elytron rather wide, convex, noticeably dilated towards middle and evenly narrowing in apical half.

Uskatocoleus uralensis Ponomarenko, sp. nov.

Plate 4, fig. 6

Etymology. From the Urals.

Holotype. PIN, no. 5276/1, direct impression of right elytron; Babintsevo locality, Orenburg Region; Severodvinian Stage.

Description (Fig. 51). The elytron is elongate, widest near the middle, narrowing in the apical one-third, more than 3.5 times longer than wide; its base is rounded; the sutural margin is almost straight in the basal half, curving weakly distally; the apex is acute, symmetrical; the external margin is curved almost from the base, so that the elytron was strongly convex. The schiza is short, one-tenth of the elytron length, located somewhat proximal to the middle of the elytron near its external one-third. The surface of the elytron is covered with small closely spaced tubercles and, basally, with large isolated tubercles.

Measurements, mm. Elytral length, 7.6; elytral width, 2.2.

Comparison. The new species is distinguished by the elytron size, largest in the genus; in the elytron shape, it is especially similar to *U. kaltanicus* Rhodendorf, 1961 and, in addition to the size, differs from it in the shorter schiza and in the straight sutural margin in the basal part.

Material. Holotype.

Uskatocoleus convexus Ponomarenko, sp. nov.

Plate 4, fig. 8

Etymology. The Latin *convexus* (convex).

Holotype. PIN, no. 3840/1205, left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 52). The elytron is rather wide, dilated from the base, widest near the middle, narrowing distally, 2.8 times longer than wide; the base is rounded; the sutural margin is more convex than the external margin; the apex is acute, symmetrical. The epipleural rim is narrow. The schiza is short, one-tenth of the elytron length, located in the middle part of the elytron, rather far from the external margin. The surface of the elytron is smooth.

Measurements, mm. Elytral length, 2.5–2.7; elytral width, 0.9–10.

Comparison. The new species is especially similar in size and proportions of the elytron to *U. janischewskyi* Rhodendorf, 1961 and differs from it in the shorter schiza, narrow epipleural rim, and smooth elytron surface.

Material. Holotype and paratypes PIN, nos. 3840/1204 and 1207, elytra from the same locality.

Fig. 53. *Uskatocoleus sukhonenis* sp. nov., holotype PIN, no. 3840/1273, elytron; Isady locality, Vologda Region; Severodvinian Stage.

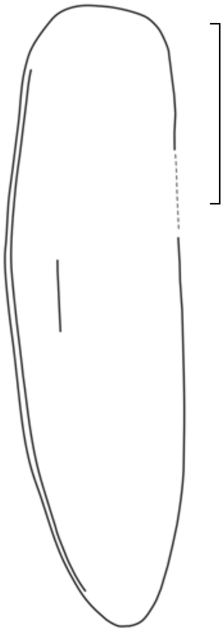


Fig. 54. *Uskatocoleus micron* sp. nov., holotype PIN, no. 3840/417, elytron; Isady locality, Vologda Region; Severodvinian Stage.

Uskatocoleus sukhonenis Ponomarenko, sp. nov.

Plate 4, fig. 7

Etymology. From the Sukhona River.

Holotype. PIN, no. 3840/1273, right elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 53). The elytron is rather wide, dilated from the base, widest near the middle, narrowing distally, 2.6–2.8 times longer than wide; the base is oblique; the sutural margin is less convex than the external margin; the apex is acute, symmetrical. The epipleural rim is narrow. The schiza is short, one-tenth of the elytron length, located proximal to the middle of the elytron, rather close to the external margin. The elytron surface is smooth.

Measurements, mm. Elytral length, 2.2–2.5; elytral width, 0.8–0.9.

Comparison. In the size and proportions of the elytron, the new species is especially similar to *U. lutugini* Rhodendorf, 1961 and differs from it in the longer schiza and less convex margins of the elytron.

Material. Holotype and paratypes PIN, nos. 3840/1206, 1269, 1270, and 1601, elytra from the same locality.

Uskatocoleus micron Ponomarenko, sp. nov.

Plate 4, fig. 9

Etymology. From the English *micron*.

Holotype. PIN, no. 3840/417, left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 54). The elytron is elongate, dilated from the base, widest near the middle, narrowing distally, 3.7 times longer than wide; the base is rounded; the sutural margin is almost straight basally and weakly curved distally; the apex is blunt, symmetrical. The schiza is rather long, one-eighth of the elytron length, located somewhat proximal to the middle of the elytron, near its external one-third. The elytron surface is smooth.

Measurements, mm. Elytral length, 2.5; elytral width, 0.7.

Comparison. In the proportions of the elytron, the new species is especially similar to *U. kishejakovicus* Rhodendorf, 1961 differs and from it in the half as large size, the shorter schiza, less protruding apical part of the elytron, and in the basally straight sutural margin.

Material. Holotype.

Genus *Pseudochrysomelites* Handlirsch, 1906

Pseudochrysomelites: Handlirsch, 1906, p. 400.

Type species. *Pseudochrysomelites rothenbachi* Handlirsch, 1906, Keuper of Switzerland, by original monotypy.

Diagnosis. Isolated elytra of small beetles. Elytron wide, with external margin in apical one-third only slightly convex, or, more often, straightly truncated. Elytral apex asymmetrical; sutural margin almost straight. Elytron surface smooth, without large punctures, only with fine punctation. Schiza usually invisible.

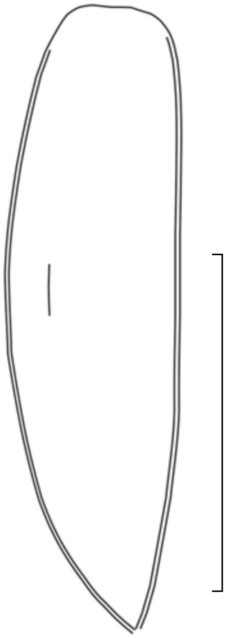


Fig. 55. *Pseudochrysomelites longus* sp. nov., holotype PIN, no. 3840/1208, elytron; Isady locality, Vologda Region; Severodvinian Stage.

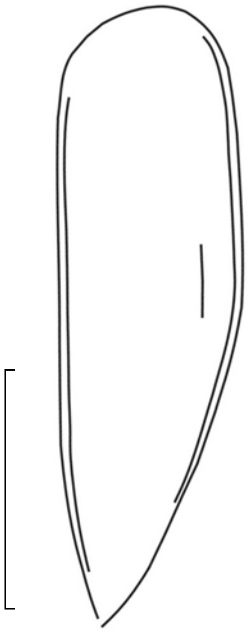


Fig. 56. *Pseudochrysomelites medialis* sp. nov., holotype PIN, no. 3840/1671, elytron; Isady locality, Vologda Region; Severodvinian Stage.

Species composition. In addition to the holotype, previously described but unnamed "species" 5, 23, and 25 from the Anisian of northeastern France (Papier et al., 2005) should be referred to this genus; a similar elytron shape is also observed in "species" 2, but fine grooves are described on its disc. The species *Palademosyne ovum* Ponomarenko, 2004, *P. elongatum* Ponomarenko, 2004, and *P. latum* Ponomarenko, 2004 should also be transferred to this genus. These forms were previously described as members of the genus *Palademosyne* Rohdendorf, 1961, but they differ considerably from the type species of this genus in the almost straight sutural margin and the apex shifted towards it. This elytral shape is especially characteristic of Early Triassic beetles.

Comparison. The genus is distinguished by the straight posterior margin of the elytron, so that the elytral apex seems asymmetrical.

Pseudochrysomelites longus Ponomarenko, sp. nov.

Plate 4, fig. 10

Etymology. The Latin *longus* (long).

Holotype. PIN, no. 3840/1208, left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 55). The elytron is elongate, narrowed distally in the apical one-third, noticeably more strongly narrowed near the apex, but the inflection of the external margin, which is characteristic of the genus, is weak; the apex is pointed; the sutural margin is bordered; the epipleural rim is narrow. The elytron base is straight. The length-to-width ratio of the elytron is 3.4 : 1. The schiza is short, located in front of the middle of the elytron. The elytron surface is smooth.

Measurements, mm. Elytral length, 1.7; elytral width, 0.5.

Comparison. The new species is distinguished by the elongate elytron and weak inflection of its external margin, which makes it close to the Triassic *Pseudochrysomelites anser* Ponomarenko, 2008, but the new species has a narrower elytron than that species and its base is straight and the apex is nonprotruding.

Material. Holotype.

Pseudochrysomelites medialis Ponomarenko, sp. nov.

Plate 4, fig. 11

Etymology. The Latin *medialis* (middle).

Holotype. PIN, no. 3840/1671, right elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 56). The elytron is elongate, narrowed distally in the apical one-third; the inflection of the external margin, which is characteristic of the genus, is weak; the apex is pointed; the sutural margin is bordered; the epipleural rim is narrow. The elytron base is oblique. The length-to-width ratio of the elytron is 3.4 : 1. The schiza is short, located in front of the middle of the elytron. The elytron surface is smooth.

Measurements, mm. Elytral length, 2.4; elytral width, 0.7.

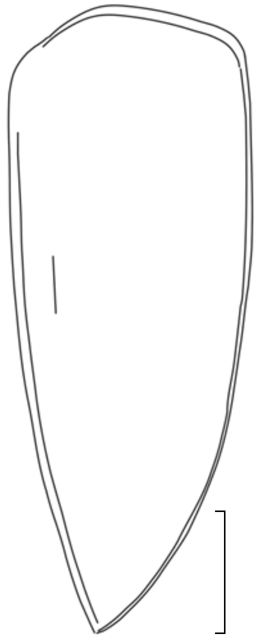


Fig. 57. *Pseudochrysomelites sphenoidalis* sp. nov., holotype PIN, no. 3840/1268, elytron; Isady locality, Vologda Region; Severodvinian Stage.

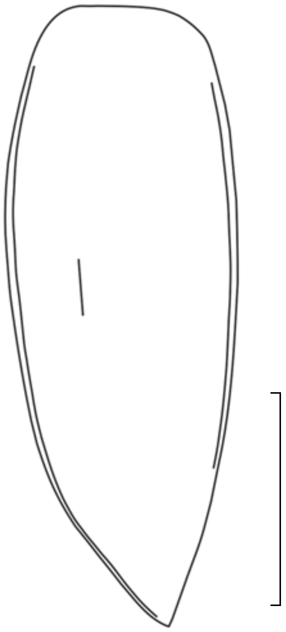


Fig. 58. *Pseudochrysomelites bashkuevi* sp. nov., holotype PIN, no. 3840/1276, elytron; Isady locality, Vologda Region; Severodvinian Stage.

Comparison. The new species is distinguished by the narrow, elongate elytron and weak inflection of its external margin, which makes it similar to *Pseudochrysomelites longus* sp. nov.; however, in the new species, the elytron is much larger, narrowed from the middle, and has an oblique base.

Material. Holotype.

Pseudochrysomelites sphenoidalis Ponomarenko, sp. nov.

Plate 4, fig. 12

Etymology. From the Greek *sphen* (wedge).

Holotype. PIN, no. 3840/1268, right elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 57). The elytron is rather wide, narrowed distally almost from the base, more strongly narrowed near the apex, but the inflection of the external margin, which is characteristic of the genus, is weakly pronounced; the apex is pointed, asymmetrical, shifted towards the sutural margin; the sutural margin is bordered; the epipleural rim is narrow. The base of the elytron is convex. The length-to-width ratio of the elytron is 3.1 : 1. The schiza is short, located in front of the middle of the elytron. The elytron surface is smooth.

Measurements, mm. Elytral length, 2.8; elytral width, 0.9.

Comparison. The new species differs from all congeners in the wedge-shaped elytron, narrowed almost from the base.

Material. Holotype.

Pseudochrysomelites bashkuevi Ponomarenko, sp. nov.

Plate 4, fig. 13

Etymology. In honor of the paleoentomologist A.S. Bashkuev.

Holotype. PIN, no. 3840/1276, left elytron; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 58). The elytron is rather wide, dilated from the base, narrowed distally in the apical half, more strongly narrowed near the apex; the inflection of the external margin, which is characteristic of the genus, is clearly pronounced; the apex is pointed, noticeably shifted farther from the sutural margin; the sutural margin is bordered; the epipleural rim is narrow. The elytron base is convex. The length-to-width ratio of the elytron is 3.5 : 1. The schiza is short, located in front of the middle of the elytron. The elytron surface is smooth.

Measurements, mm. Elytral length, 2.9; elytral width, 1.0.

Comparison. The new species differs from congeners in the convex external margin of the elytron and the inflection of the external margin, which makes it similar to Triassic *Pseudochrysomelites anser* Ponomarenko, 2008; however, in the new species, the elytron base is straight and the apex is nonprotruding.

Material. Holotype.

Schizophoridae Ponomarenko, 1968

Schizophoridae incertae sedis

The specimen described below (PIN, no. 3286/142) from the Middle Permian Chepanikha locality has smooth elytra and, based on the presence of other parts of the body, should be treated in the family Schizophoridae. Only one schizophorid has previously been described from the Permian, *Dikerocoleus* Lin, 1982 from the Middle to Upper Permian of China, but the morphology of its underside has not been described and the specimen in question lacks head and pronotum. Thus, consistent comparison of the two specimens is impossible, although they probably belong to different species.

Description (Fig. 59; Pl. 4, fig. 14). A rather small, elongate oval, flattened beetle. The mesepimeron is transverse. The mesocoxa is longer than wide. The metaventrite is transverse, occupies most of the metathorax, twice wider at the posterior margin than long; its lateral margins are very weakly rounded. The metepisterna reach the mesocoxal cavity and are strongly, but gradually anteriorly dilated; their anterior margin is twice as wide as the posterior margin. The metacoxae completely separate the metaventrite and abdomen and are much wider than long. The elytra are narrow, thrice longer than wide, narrowed in their apical half. The schiza is invisible. The entire body is covered with small closely spaced tubercles.

Measurements, mm. Body length, about 5; body width, 1.6; elytral length, 4.

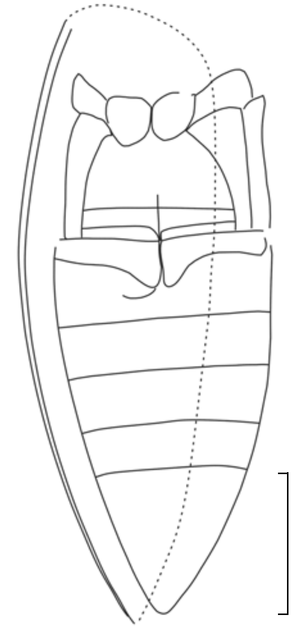


Fig. 59. Schizophoridae incertae sedis, specimen PIN, no. 3286/142, habitus in ventral view; Chepanikha locality, Udmurtia; Urzhumian Stage.

2.4. New Permochoristidae (Insecta: Mecoptera) from the Isady Locality

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The chapter describes new mecopterans of the family Permochoristidae from the Isady locality: *Agetopanorpa danili* sp. nov., *Neudolbenus kopylovi* gen. et sp. nov., *N. giganteus* sp. nov., *Tatarakara variomaculata* sp. nov., *Mesochorista generalis* sp. nov., *Permeca pygmaea* sp. nov., and *P. media* sp. nov.

An overview of the mecopteran assemblage of Isady is given in Chapter 1.2.3.

Since all material was collected in the same locality, the geographic and stratigraphic position of which are characterized above, detailed geographic and stratigraphic data are omitted in the descriptions. The vein nomenclature follows Novokshonov (1997).

The material is stored in the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN).

Family Permochoristidae Tillyard, 1917

Subfamily Agetopanorpinae Carpenter, 1930

Genus *Ageropanorpa* Carpenter, 1930

Ageropanorpa danili **Bashkuev, sp. nov.**

Etymology. In honor of the paleoentomologist D.S. Aristov.

Holotype. PIN, no. 3840/1527; part and counterpart of forewing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 60a, 60b, 62a, 62b). The wing is relatively wide, almost symmetrical, with a rounded apex. SC has one long inclined branch. The costal and subcostal spaces are equally wide. R has a deep ladle-shaped curve distally and an oblique anterior branch. The pterostigma is weak, poorly pronounced. The stem of MP is desclerotized over almost half of its length proximal to the bifurcation; thyridulum is absent. MP is five- or six-branched, with forks on MP_1 (absent in paratype PIN, no. 3840/709) and MP_2; MP_3 and MP_4 are simple. The free base of CuA and the base of M_5 are equally well developed, forming a regular “Y-vein.” Crossveins in the cubito-anal area are located stepwise, at the same inclination and at equal distances from each other. The wing is not pigmented.

Measurements, mm. Holotype: wing length, 6; width, 2.6; paratypes: PIN, no. 3840/709: wing length, ca. 5.2; width, ca. 2; PIN, no. 3840/1532: wing length, ca. 6; width, ca. 2.3.

Comparison. The new species is the only species of the genus with one branch of SC. It is most sim-

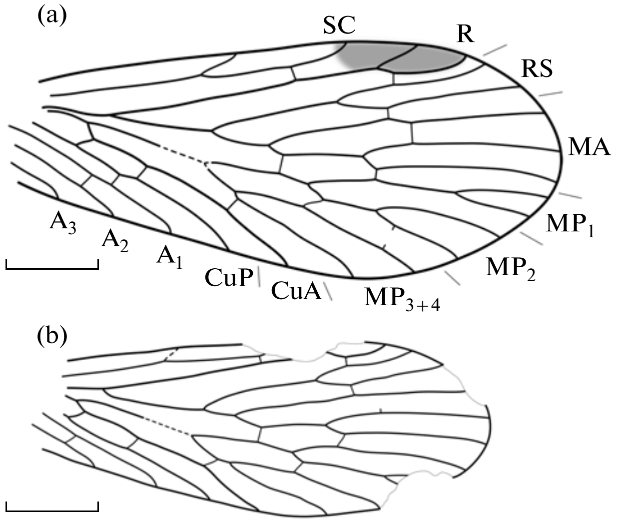

Fig. 60. *Agetopanorpa danili* sp. nov.: (a) holotype PIN, no. 3840/1527; (b) paratype PIN, no. 3840/709. Scale bar, 1 mm.

ilar to *Agetopanorpa similis* (Riek, 1973) from the Upper Permian of South Africa, from which it can be distinguished by different shapes of SC and R. It differs from all Lower and Middle Permian species in the branching of MP with forked MP_1 and simple MP_4 and from Upper Permian species of Australia in the wider wing.

Material. In addition to the holotype, paratypes PIN, nos. 3840/709 (Fig. 60b) and 1532.

Subfamily Permochoristinae Tillyard, 1917

Tribe Petromanteini Martynova, 1961

Genus *Neudolbenus* Bashkuev, gen. nov.

Etymology. Arbitrary combination of letters. Gender masculine.

Type species. *Neudolbenus kopylovi* sp. nov.

Diagnosis. SC long, with two distal closely positioned branches. RS and MA with two branches. MP with six branches. Base of CuA strong, strongly inclined. Anal area elongate, with four long, straight, parallel anal veins. Hindwings unknown.

Species composition. In addition to the type species, *N. giganteus* sp. nov.

Comparison. The new genus is sharply distinguished from other genera of the family by the structure of the anal area.

Neudolbenus kopylovi Bashkuev, sp. nov.

Etymology. In honor of the paleoentomologist D.S. Kopylov.

Holotype. PIN, no. 3840/745; part and counterpart of forewing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 61a, 61b, 62c, 62d). The forewing is elongated oval. The branches of SC are inclined, approaching each other; the proximal branch diverges proximal to the bifurcation of RS + MA; the distal branch diverges distal to this bifurcation. The pterostigma is lanceolate, elongate, with an almost straight posterior margin. The stem RS + MA is long, almost equal in length to the stem of RS. Both RS and MA are two-branched; the RS fork is rather deep, but noticeably shorter than that of MA. The MP stem is almost one-third of the wing length. The thyridium is rather small; the thyridulum is absent. The base of CuA is strong, strongly inclined, curved or sigmoid. M_5 is short, almost reduced. CuA and CuP approach each other at the point where the crossvein cua–cup is attached. CuP in the apical part is bent sharply posteriad. Four simple, very long, straight anal veins are positioned in parallel, with A_1 reaching the middle of the wing, and A_4 running subparallel to the posterior margin and reaching the level of RS + MA origin. Crossveins are numerous, mostly weak or desclerotized (except for distinct sigmoid a_1–a_2 and short vertical cua–cup). Coloration is intense, finely spotted.

Measurements, mm. Holotype: wing length, 9; paratype PIN, no. 3840/241: wing length, presumably about 9.6 (length of preserved part, 8.5); paratype PIN, no. 3840/1390, wing length, presumably about 7.5 (length of preserved part, 6.7).

Material. In addition to the holotype, paratypes PIN, nos. 3840/241 and 1390 from the same locality.

Neudolbenus giganteus Bashkuev, sp. nov.

Etymology. The Latin *giganteus* (gigantic).

Holotype. PIN, no. 3840/1391; base of forewing (part and counterpart); Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 62e, 62f). The anterior margin has a convexity in the basal part. The venation of the preserved wing fragment fully complies with that of *N. kopylovi*. A distinct, long humeral vein is present. The crossvein cup–a_1 is absent. The wing membrane is compact, densely pigmented, with small irregular light spots.

Measurements, mm. Length of preserved part, 7; presumable total wing length, at least 17.

Comparison. The new species differs from *N. kopylovi* in the very large size (at least twice as large).

Material. Holotype.

Tribe Mesochoristini Martynova, 1961

Genus *Tatarakara* Novokshonov, 1995

Type species. *Tatarakara maculata* Novokshonov, 1995; eastern Kazakhstan; ?Upper Permian.

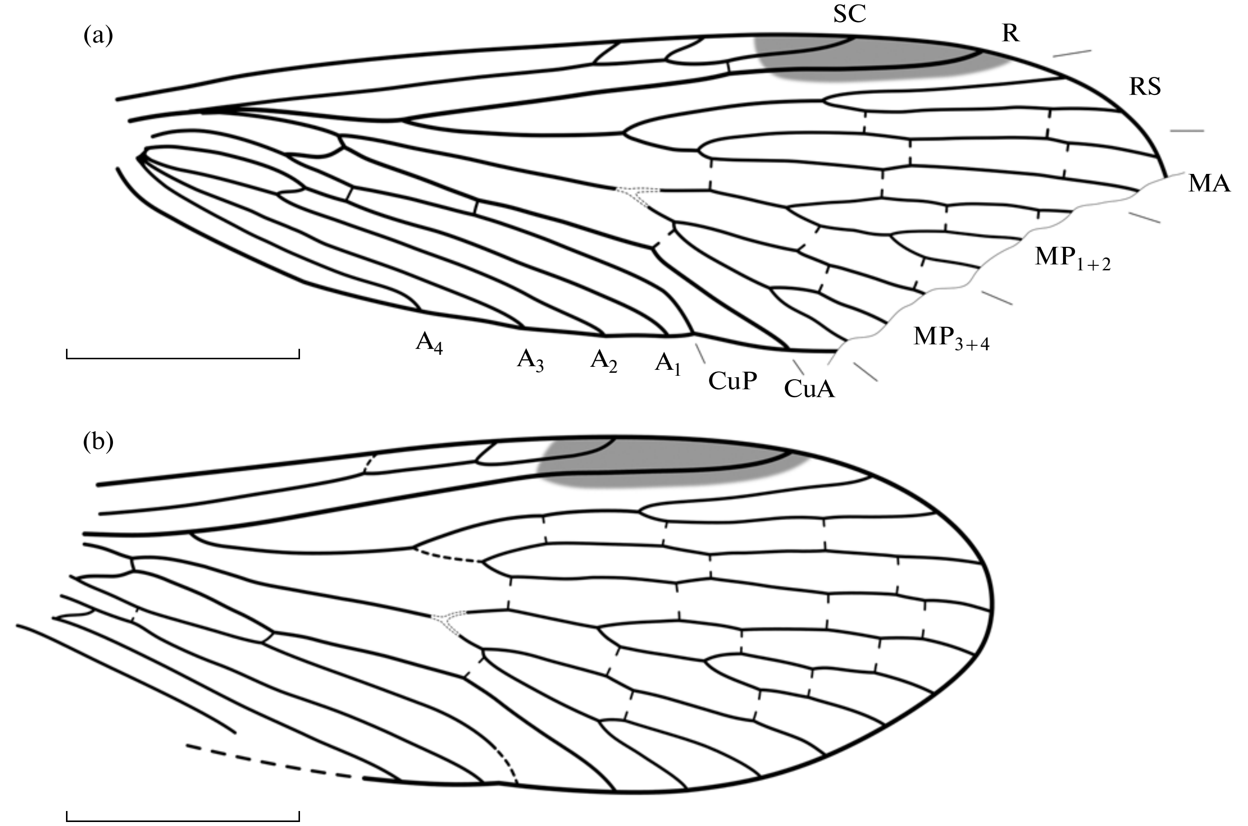

Fig. 61. *Neudolbenus kopylovi* gen. et sp. nov.: (a) holotype PIN, no. 3840/745; (b) paratype PIN, no. 3840/241. Scale bar, 2 mm.

Species composition. In addition to the type species, *T. variomaculata* sp. nov. from the Isady locality, described below.

Remarks. In his description of the genus *Tatarakara,* Novokshonov (1995, 1997) indicated as its main difference from *Mesochorista* Tillyard, 1916 the presence of two anterior branches in SC, the basal of which is located proximal to the base of RS + MA. Doing so, he used only Permian and some Triassic species of *Mesochorista* (sensu lato), excluding from his analysis most of the Mesozoic taxa, for which the said difference does not hold true. For instance, the proximal position of the first branch of SC (even more pronounced than in *Tatarakara*) is found in *Mesochorista sinuata* (Handlirsch, 1939) from the Lias of Germany (Ansorge, 1995). This selectivity resulted in the obvious impossibility to use the taxa established by Novokshonov with regard to Mesozoic material. Establishing the precise taxonomic position of this genus and other genera close to *Mesochorista* and possibly its junior synonyms (*Liassochorista* Tillyard, 1933, *Kazakhopanorpa* Novokshonov, 1995, *Qingochorista* Guo et Hong, 2003, and others) would require a large-scale revision of both Permian and Mesozoic material. Such a revision is beyond the scope of this study. I follow here the opinion of Novokshonov, formally understanding *Tatarakara* as a separate genus, taking into account the said Remarks.

Tatarakara variomaculata Bashkuev, sp. nov.

Etymology. From the Latin *varia* (various) and *maculata* (spotted).

Holotype. PIN, no. 3840/1427; positive impression of forewing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 63a–63j, 66a–66f). The forewing is oval, with a smoothly convex anterior margin and a rounded apex. The costal space is relatively narrow; the subcostal space is wide. SC is long, with two short anterior branches, the basal of which diverges proximal to the base of RS + MA; SC at the point where its distal branch diverges bends towards R and is connected with it at the basal margin of the pterostigma by a very short crossvein; at this point, R bends sharply posteriad. The pterostigma is distinct, with an oblique basal margin. The base of RS_2 is partly or completely desclerotized, as well as the crossvein rs_2–ma_1. The thyridium is localized in one point. The base of CuA is long, inclined; the base of M_5 is short or absent; if absent, CuA joins MP in one point or fuses with it over a short distance. Crossveins are rather infrequent, weak or desclerotized; they are stable in

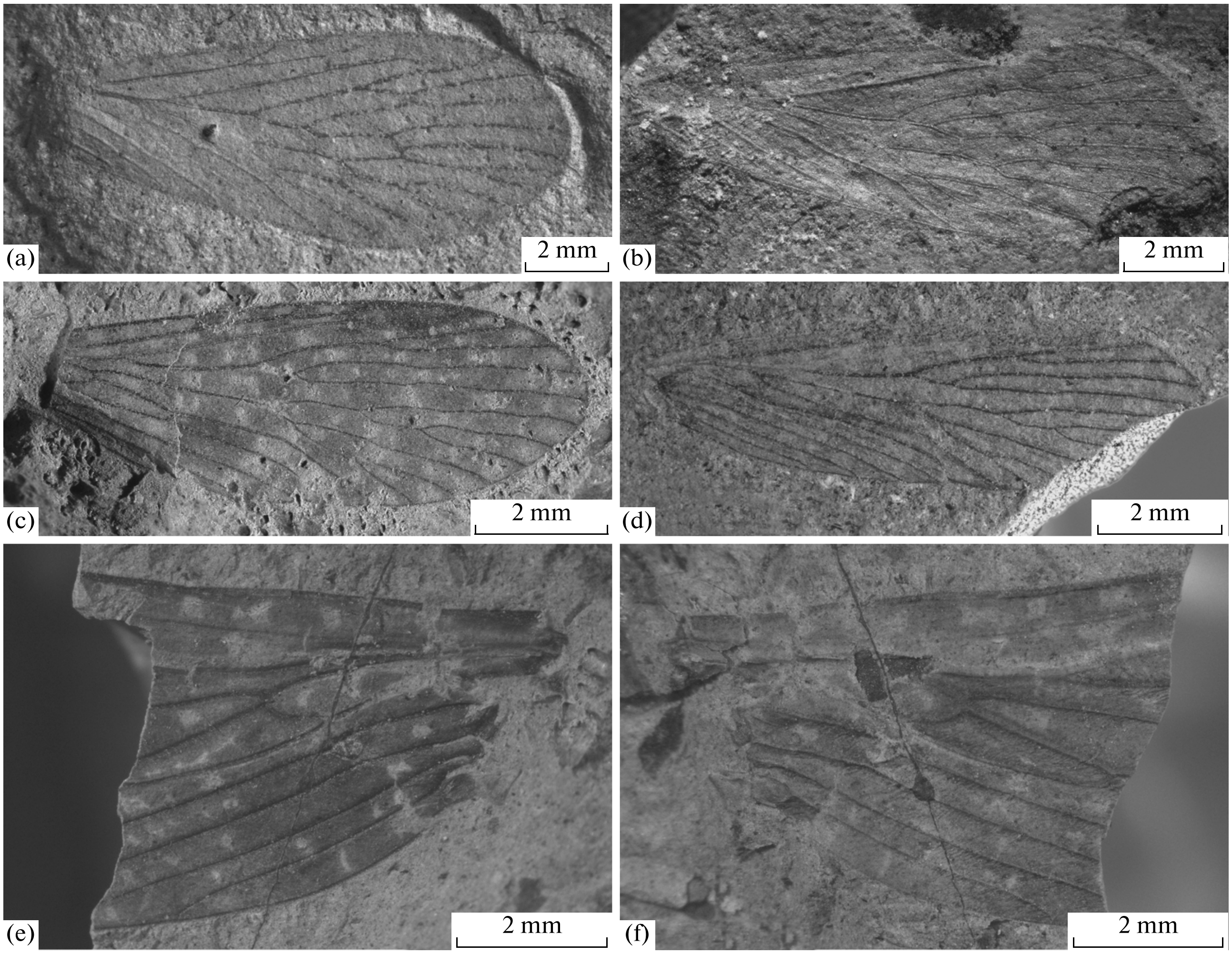

Fig. 62. New taxa of Permochoristidae: (a, b) *Agetopanorpa danili* sp. nov.: (a) holotype PIN, no. 3840/1527; (b) paratype PIN, no. 3840/709; (c, d) *Neudolbenus kopylovi* gen. et sp. nov.: (c) paratype PIN, no. 3840/241, photomontage of counterpart and mirror image of part; (d) holotype PIN, no. 3840/745, mirror image; (e, f) *Neudolbenus giganteus* sp. nov., holotype PIN, no. 3840/1391, part and counterpart.

position, varying within a narrow range: there are six veins between the branches of RS, MA, and MP, as well as mp_4–cua, cua–cup, and a_1–a_2. The coloration is represented by many spots, the shape and size of which vary rather widely, but the general pattern remains the same (Figs. 63a, 63b, 63d). In the hindwing, SC is shortened, reaches the costal wing margin near the wing's middle; sometimes, a very weak vestigial vein that joins the apex of SC with R is preserved (Fig. 66e). MP is four-branched (very rarely, five-branched, with an additional fork on MP_2); the bases of RS_2, MA_1, and MA_2 are desclerotized; the thyridium is shifted proximad onto the stem MP. In the anal area, the space between A_1 and A_2 is extremely wide, crossed by a very long crossvein a_1–a_2; A_2 is shifted basally and positioned closer to A_3.

Measurements, mm. Forewing length, 4.9–7.7 (holotype 6.5).

Variability. The shape and size of the wing, coloration and the type of fusion between CuA and MP vary rather widely (Figs. 63a–63h), while the position of the main vein systems is very stable. Sometimes, short additional forks of the branches of MP occur.

Comparison. The new species differs from the type species in the desclerotized base of RS_2 and SC running closer to R and in the more blurred coloration, without distinct rows of spots between the longitudinal veins.

Material. In addition to the holotype, paratypes PIN, nos. 3840/82, 85, 88, 89, 338, 379, 759–764, 768, 777, 1305, 1428–1444, 1446–1448, 1450, 1451, 1453–1456, 1458, 1459, 1461, forewings; 3840/77, 81, 87, 299, 401, 765–767, 769, 770, 773, 775, 780, 789, 1466–1469, 1471–1476, 1478–1483, and 2550, hindwings; and 30 forewings and 15 hindwings not included in the type series because of their poor preservation.

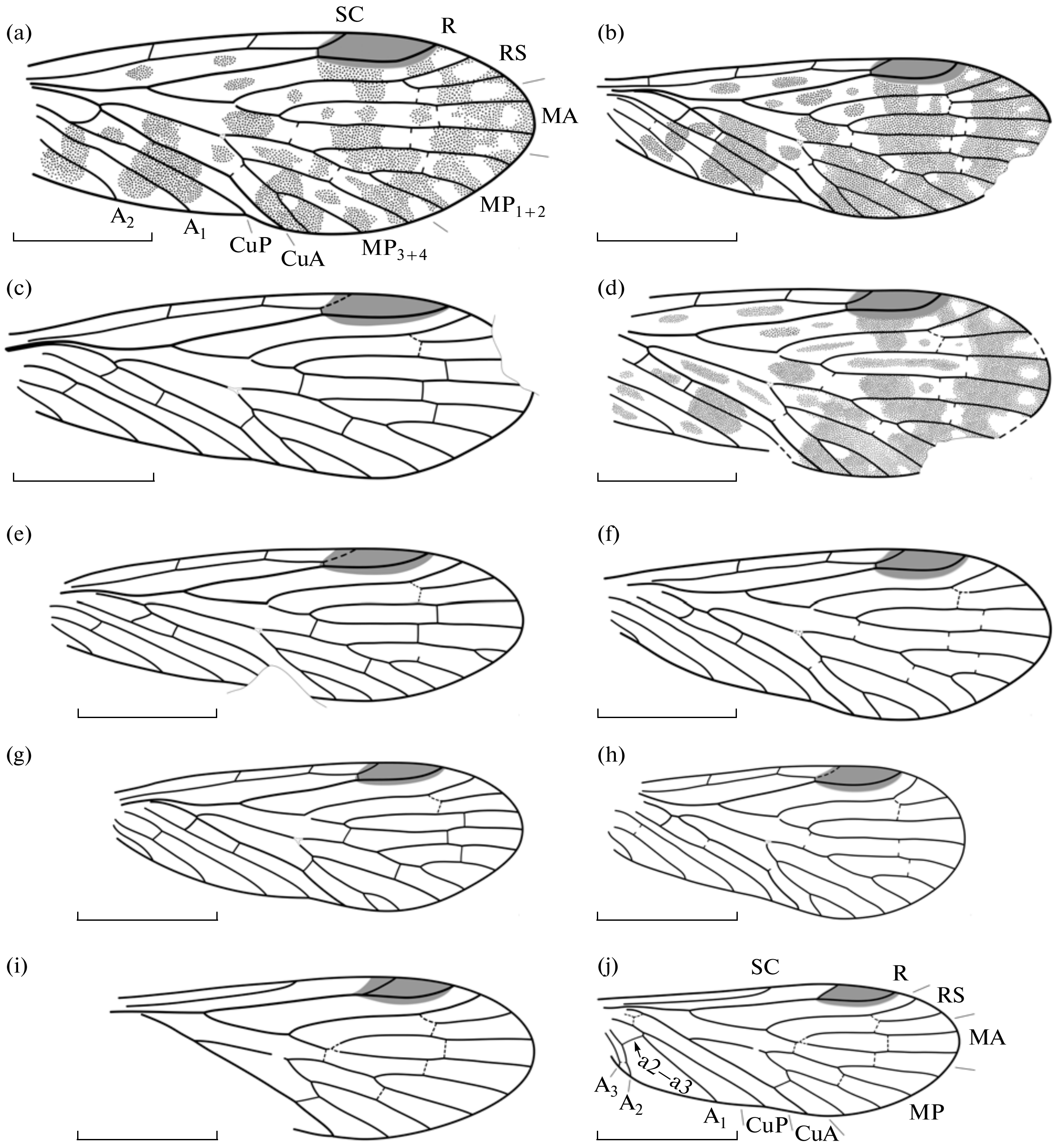

Fig. 63. *Tatarakara variomaculata* sp. nov.: (a) holotype PIN, no. 3840/1427, forewing; (b–h) paratypes, forewings: (b) PIN, no. 3840/1428; (c) PIN, no. 3840/763; (d) PIN, no. 3840/1436; (e) PIN, no. 3840/338; (f) PIN, no. 3840/1441; (g) PIN, no. 3840/768; (h) PIN, no. 3840/1434; (i, j) hindwings: (i) paratype PIN, no. 3840/766; (j) paratype PIN, no. 3840/1467. Scale bar, 2 mm.

Genus *Mesochorista* Tillyard, 1916

Mesochorista generalis Bashkuev, sp. nov.

Etymology. From the Latin *generalis* (generic).

Holotype. PIN, no. 3840/1421, part and counterpart of forewing without base; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 64a–64d, 66g, 66h). The forewing is oval, almost symmetrical. The anterior margin is smoothly convex. SC is long, passing far into the pterostigmal area, with one anterior branch located approximately at the level of the middle of the stem RS + MA. Proximal to the branch of SC, the costal space is narrower than the subcostal space, then, dilating. The crossvein sc-r is located at the level of the bifurcation of MA. R curves smoothly distally. The pterostigma is distinct, with an oblique basal margin.

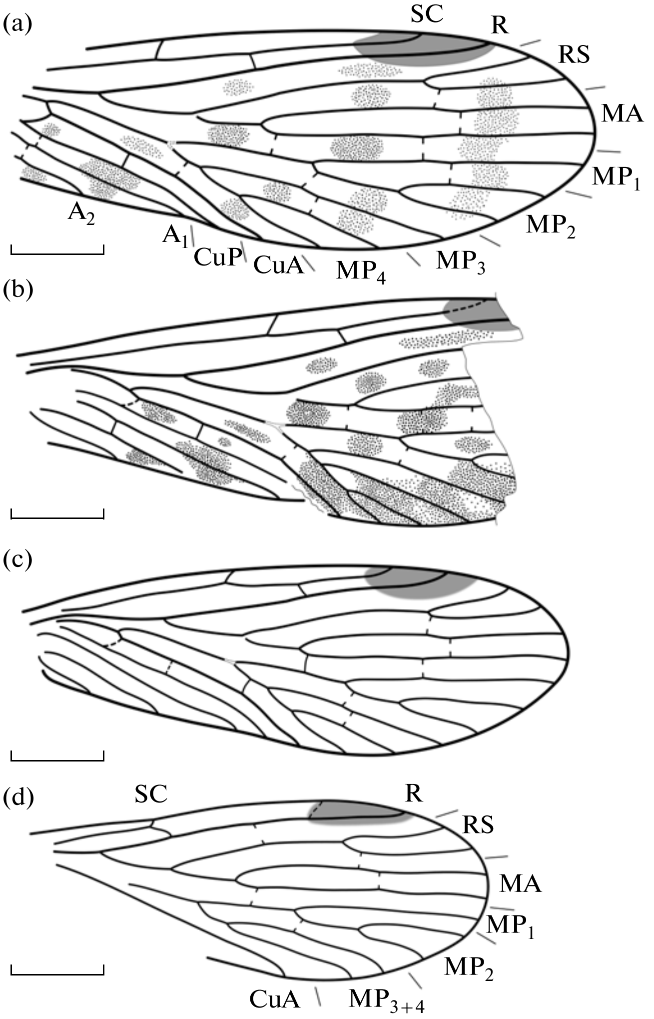

Fig. 64. *Mesochorista generalis* sp. nov.: (a) holotype PIN, no. 3840/1421; (b) paratype PIN, no. 3840/509; (c) paratype PIN, no. 3840/79; (d) paratype PIN, no. 3840/786, hindwing. Scale bar, 1 mm.

RS + MA and MP branch rather proximally, significantly proximal to the middle of the wing length. The stem RS$_{1+2}$ is weakly S-shaped. The fork of RS is half as long as the fork of MA. MP is normally six-branched. The base of M$_5$ is distinct, relatively long; the base of CuA is oblique, curved. Crossveins are rather infrequent, weak. All longitudinal veins are covered with closely spaced, regularly arranged tubercles (bases of setae). The wing coloration resembles that of *Tatarakara variomaculata,* but is somewhat less intense, especially distally. In the hindwing, SC reaches the proximal one-third of the wing, ending in an asymmetrical fork. MP has five branches (with a bifurcation in MP$_2$).

Measurements, mm. Forewing length, 6.1–7; forewing width, 2.15–2.5.

Variability. The shape and size of spots vary somewhat; paratypes PIN, nos. 3840/79 and 1493 have additional bifurcations in branch MP$_4$; in paratype PIN, no. 3840/1426, MP has five branches (MP$_2$ simple).

Comparison. The new species differs from the closest species *Mesochorista australica* (Tillyard, 1917) (according to Riek, 1953, text-figs. 8–17) in the more basal position of the anterior branch of SC and in the distinctly curved base of MP.

Material. In addition to the holotype, paratypes PIN, nos. 3840/79, 83, 407, 509, 755, 758, 1423–1426, 1493, forewings; 3840/786, hindwing; and 3840/1422, three wings and body fragment.

Genus *Permeca* Novokshonov, 1995

Type species. *Permeca tatarica* Novokshonov, 1995; eastern Kazakhstan; Upper Permian.

Emended diagnosis. SC long, ending in pterostigmal area, with one short branch, diverging before RS + MA origin. Crossvein sc–r located approximately at middle of distal segment of SC. Pterostigma distinct, semicircular. RS fork much shorter than MA fork. MP five- or six-branched. Connection between CuA and MP Y-shaped, base of CuA strongly inclined. Longitudinal veins covered with large, regularly arranged tubercles. Wing coloration rather intense, variegated. Hindwings unknown.

Species composition. In addition to the type species, *P. pygmaea* sp. nov. and *P. media* sp. nov. from the Isady locality (see below).

Comparison. The genus in question differs from the closest genus *Mesochorista* in the single basally located branch of SC.

Permeca pygmaea Bashkuev, sp. nov.

Etymology. From the latinized Greek *pygmaeus* (dwarf).

Holotype. PIN, no. 3840/240, forewing and body fragment (part and counterpart); Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 65b; 66j). The wing is short (length-to-width ratio is about 2.65), with a blunt apex. The branch of SC diverges very proximally, much more so than the base of RS + MA, drawing SC to the anterior wing margin; the subcostal space in this area is strongly dilated. MP is five-branched (with simple MP$_2$). The base of M$_5$ is relatively short; the base of CuA is inclined almost horizontally. Crossveins are weak and widely spaced. The costal wing margin is densely pubescent. The coloration of the wing is spotted, intense, especially distally.

Measurements, mm. Holotype: forewing length, 3.45; forewing width, 1.3; paratype PIN, no. 3840/1420: length, 3.28; width, 1.1.

Comparison. The new species differs from the two other species of the genus in the very small size and the strongly shortened wing; it also differs from *P. tatarica* in the much more proximal position of the branch of SC.

Material. In addition to the holotype, paratypes PIN, nos. 3840/1419 (wing fragment), 1420 (complete wing).

Permeca media Bashkuev, sp. nov.

Etymology. From the *medius* Latin (middle).

Holotype. PIN, no. 3840/588, forewing (part and counterpart); Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 65a; 66i). The wing is narrow and elongate (length-to-width ratio is about 3.2). The branch of SC diverges much more proximally than the base of RS + MA; the costal space is narrowed in the area where the anterior branch of SC diverges; the subcostal space is slightly dilated. MP is five-branched (with simple MP_2). The base of M_5 is relatively long; the base of CuA is noticeably inclined. Crossveins are weak, widely spaced. The costal wing margin is densely pubescent. The coloration is intense, spotted.

Measurements, mm. Holotype: forewing length, 5.1; forewing width, 1.58; paratypes: PIN, no. 3840/1418: length, ca. 4.3 (length of preserved part 4.1); width, 1.32; PIN, no. 3840/752: length, 5.35; width, 1.66.

Comparison. The new species differs from congeners in the narrow and elongate wing; it also differs from *P. tatarica* in the much more basal position of the branch of SC and from *P. pygmaea* in the significantly larger size.

Material. In addition to the holotype, paratypes PIN, nos. 3840/752, 1418.

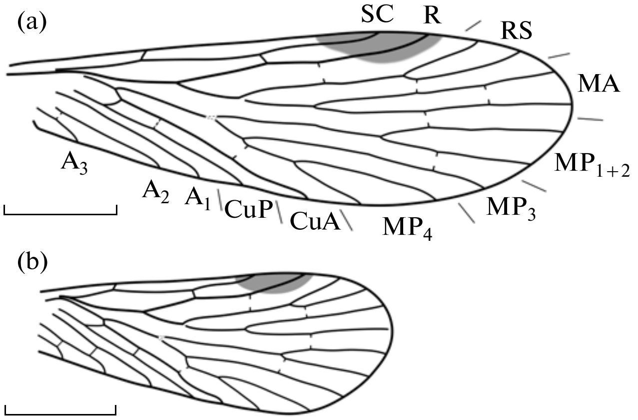

Fig. 65. *Permeca* gen. nov.: (a) *P. media* sp. nov., holotype PIN, no. 3840/588; (b) *P. pygmaea* sp. nov., holotype PIN, no. 3840/240. Scale bar, 1 mm.

2.5. New Caddisflies of the Suborder Protomeropina (Insecta: Trichoptera) from the Permian of Russia

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New members of the suborder Protomeropina are described from the Middle and Upper Permian of European Russia: *Kamopanorpa maculata* sp. nov., *K. tshepanikhensis* sp. nov. (family Microptysmatidae, Chepanikha locality, Udmurtia; Urzhumian Stage), *Cladochorista issadica* sp. nov., *Cladochoristella ryzhkovae* sp. nov. (family Cladochoristidae, Isady locality, Vologda Region; Severodvinian Stage; and Balymotikha, Vladimir Region; Vyatkian Stage), and *Prorhyacophila rasnitsyni* sp. nov. (family Prorhyacophilidae, Balymotikha locality, Vladimir Region; Vyatkian Stage). Members of the latter two families are the first described from the Permian of European Russia. General characteristics of the suborder Protomeropina are provided and members of the families Microptysmatidae, Uraloptismatidae, Cladochoristidae, and Prorhyacophilidae are reviewed.

The suborder Protomeropina currently includes five families: Protomeropidae, Microptysmatidae, Cladochoristidae, Uraloptysmatidae, and Prorhyacophilidae. The last family is sometimes regarded as a group of uncertain systematic position (Trichoptera incertae subordinis) due to the longer anal loop in the forewing and crossveins sometimes occurring in the costal space (Ivanov and Sukacheva, 2002). At the same time, the general venation pattern of Prorhyacophilidae is very close to the classic type of forewing venation of Recent caddisflies, particularly the family Rhyacophilidae, although without the crossveins rs–m_1 and rs–m_{1+2}. In this study, members of the families Microptysmatidae, Cladochoristidae, and Prorhyacophilidae found in the Middle and Upper Permian of European Russia are described. The second and third families are found in the Permian of this region for the first time.

The family Microptysmatidae is rather widespread in the Lower and Middle Permian of Eurasia. The earliest known members of this family come from the Sakmarian of the Czech Republic (Kukalova-Peck and Willmann, 1990). To date, the Microptysmatidae have not been found in Mesozoic deposits. This family is distinguished from the order Panorpida, ancestral to caddisflies, mainly by the absence of the anal loop in

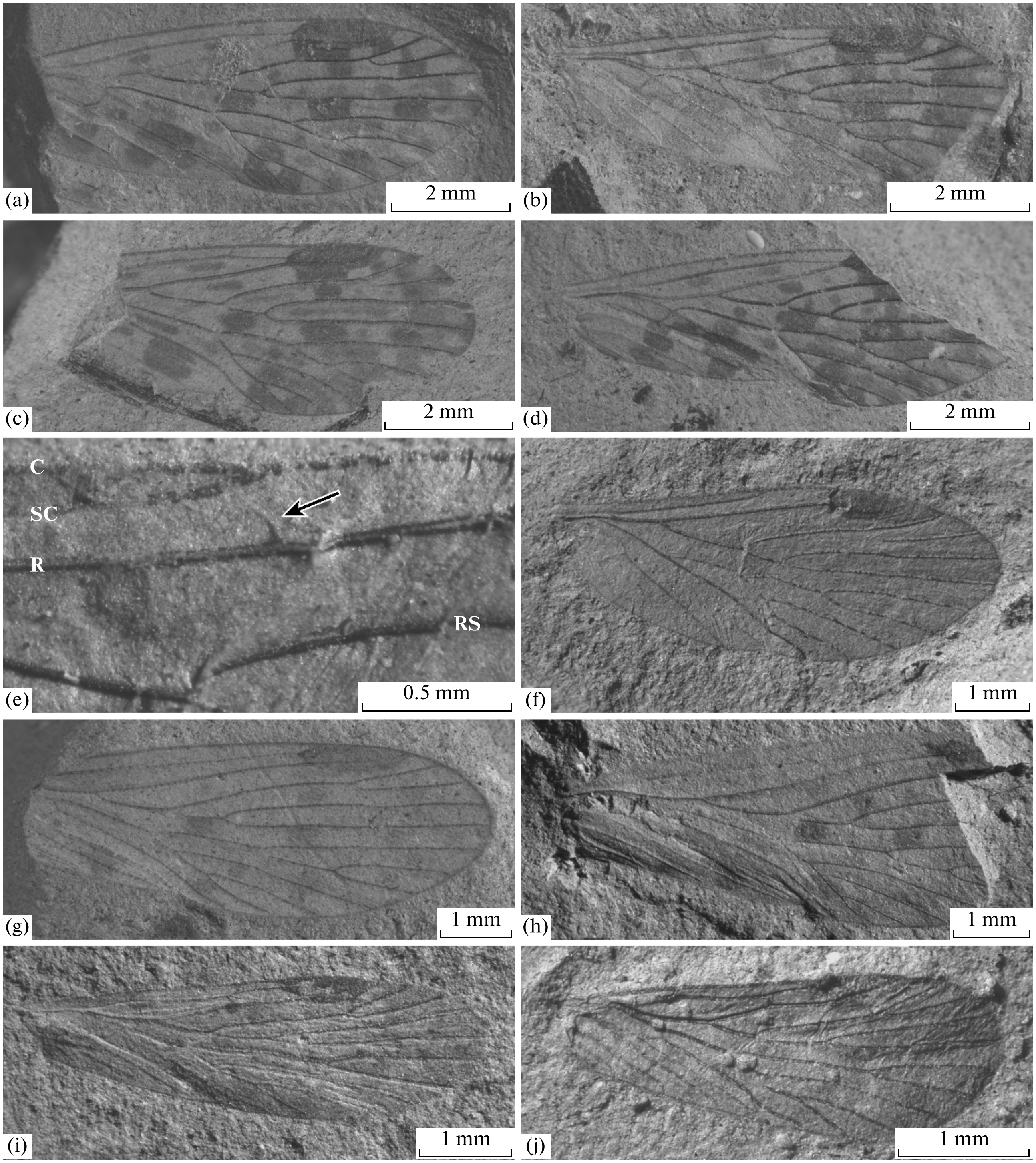

Fig. 66. New taxa of Permochoristidae: (a–f) *Tatarakara variomaculata* sp. nov.: (a) holotype PIN, no. 3840/1427, mirror image; (b) paratype PIN, no. 3840/1428; (c) paratype PIN, no. 3840/1436; (d) paratype PIN, no. 3840/1429, mirror image; (e) paratype PIN, no. 3840/87, details of hindwing venation; (f) paratype PIN, no. 3840/2550, hindwing; (g, h) *Mesochorista generalis* sp. nov.: (g) holotype PIN, no. 3840/1421; (h) paratype PIN, no. 3840/79, mirror image; (i) *Permeca media* sp. nov., holotype PIN, no. 3840/588; (j) *Permeca pygmaea* sp. nov., holotype PIN, no. 3840/240.

both wing pairs (Novokshonov, 1992). Among extant caddisflies, this feature is only found in members of the family Hydroptilidae and some species of Molannidae and Beraeidae. The causes of the emergence and function of the anal loops have been treated in detail by Ivanov (1992b). Anal loops in both wing pairs are also found in Protomeropidae, another family of the suborder, which additionally retains vestigial ends of A_2 and A_3, mostly in the forewings. They look like weak crossveins not disturbing the loop shape. To date, not only wings, but also body morphology of Protomeropidae have been studied in detail (Carpenter, 1930; Novokshonov, 1997); they retain many primitive characters shared with their presumable ancestors, early scorpionflies. Morphologically, they still only very slightly differ from Panorpida and are more similar to scorpionflies than to caddisflies (Novokshonov, 1997). Presently, Protomeropidae are known from the Lower Permian of the United States, Czech Republic, and Russia and from the Upper Permian of Kazakhstan, South Africa, and Australia.

The genus *Kamopanorpa* Martynov, 1928, which includes the microptysmatid species described in this study, was described from the Middle Permian of Tatarstan as a member of the order Mecoptera (Martynov, 1928). Subsequent detailed study of extensive new material from the Permian of European Russia has shown that forewings of *Kamopanorpa* have a distinct anal loop, characteristic of caddisflies, and the genus was transferred to the order Trichoptera (Sukatsheva, 1976). To date, 12 species of the genus *Kamopanorpa* are known, two of which, *K. maculata* sp. nov. and *K. tshepanikhensis* sp. nov., are described in this study from the Chepanikha and Kostovaty localities (Urzhumian Stage of the Middle Permian of Udmurtia). A total of six caddisfly specimens have been found in the Chepanikha locality. Five of them belong to the genus *Kamopanorpa,* including three (specimens PIN, nos. 3286/77, 79 (Fig. 67c, 69f), and 3286/122) identified only to genus. Especially rich material representing the genus *Kamopanorpa* has been collected in the Chekarda locality (Kungurian Stage of the Lower Permian of the Perm Region). The study of more than 200 specimens of *K. uralensis* (Martynov, 1940) from this locality has revealed wide variation in forewing venation, especially in RS + MA and MP (Novokshonov, 1992). This allowed Novokshonov (1992) to synonymize several species (Table 1) described by A.V. Martynov from rather poorly preserved specimens. The species *Microptismodes mongolicus* Sukacheva, 1992 from the Urzhumian Bor-Tologoi locality was transferred to the genus *Kamopanorpa* (Table 1). The typical forewing venation pattern of *Kamopanorpa* changed very little during the Permian, which is not true of the hindwing venation, the anal area of which underwent especially strong changes (Novokshonov, 1997). The wing coloration in the genus *Kamopanorpa* is species-specific. This is confirmed by our material from the Chepanikha locality. The body morphology of *Kamopanorpa* species was studied in detail by the example of *K. rotundipennis* Martynov, 1933 from the Soyana locality (Lower Kazanian Substage of the Middle Permian of the Arkhangelsk Region: Ivanov, 1988); in the same study, the main differences of adult forms of *Kamopanorpa* from extant adult caddisflies and scorpionflies were revealed.

The family Uraloptismatidae, very close in wing venation and size to Microptismatidae, but having a number of important differences from it in body morphology, was originally described from the Chekarda locality (Ivanov, 1992a). Taking into account the fact that our material includes only forewings, the wide variation of venation in the genus *Kamopanorpa,* and the clear similarity of our material to *K. grossa* Novokshonov, 1993 and *K. pritykinae* Novokshonov, 1993, we attribute the new material from Chepanikha to the more widespread family Microptismatidae rather than Uraloptismatidae, known from a single fossil from Chekarda. Ecological features of the development of the family Microptismatidae have been treated in detail by Ivanov (1992b).

The material from Isady (Vologda Region; Severodvinian Stage, Upper Permian; for more detail, see Chapter 1.2) contains two wings (forewing and hindwing) of caddisflies of the family Cladochoristidae. This family includes two genera (Table 1) and is known from impressions of forewings, the venation of which is similar in general pattern to that of living caddisflies and lepidopterans, but differs from them in the many branches of SC. From other members of the suborder Protomeropina, it is distinguished by the loss of small terminal bifurcations. The number of branches of RS + MA and MP becomes the same as in primitive Recent caddisflies (Novokshonov, 1997). Possibly, Cladochoristidae is the common ancestor of both Mesozoic–Cenozoic caddisflies and lepidopterans (Ivanov and Sukacheva, 2002). The distribution of Cladochoristidae is shown in Table 1.

The Balymotikha locality (Vladimir Region; Vyatkian Stage; for more detail, see Chapter 1.2) has yielded seven fragments of caddisfly forewings. Five of them belong to the genus *Kamopanorpa* of the family Microptismatidae (specimens PIN, nos. 5103/279–283). Two almost complete wings are described below in the families Cladochoristidae and Prorhyacophilidae. Cladochoristids are represented by *Cladochoristella ryzhkovae* sp. nov., and prorhyacophilids are represented by *Prorhyacophila rasnitsyni* sp. nov. The family Prorhyacophilidae was previously believed to be exclusively Triassic. All Prorhyacophilidae are very similar in forewing venation, varying somewhat in the position of terminal bifurcations of RS + MA and MP. The distribution of Prorhyacophilidae is shown in Table 1.

The new material expands the knowledge of occurrences of Protomeropina families and confirms the appearance of Mesozoic families of this suborder as early as the Middle Permian (Cladochoristidae) and Upper Permian (Prorhyacophilidae). In the Middle

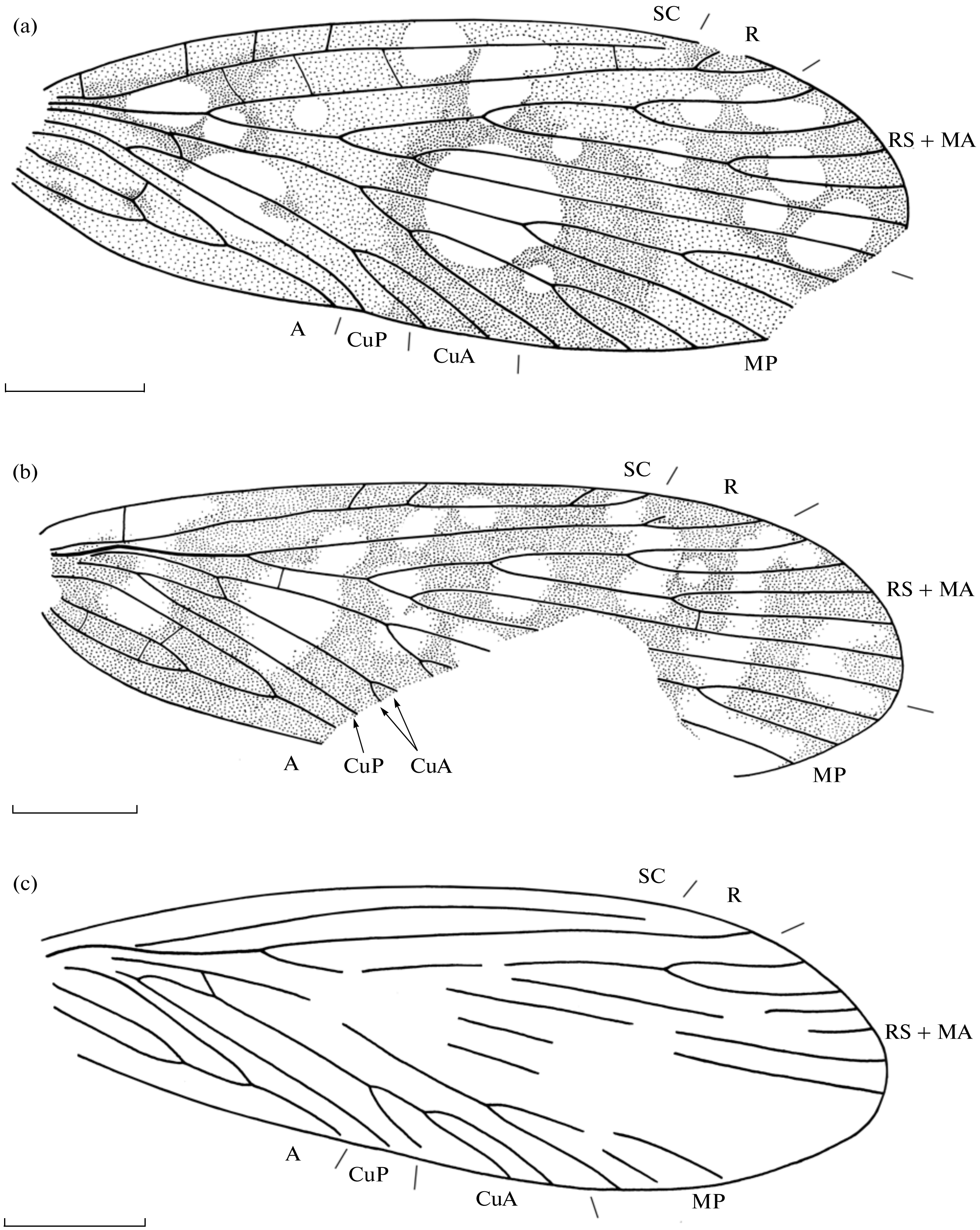

Fig. 67. New members of the genus *Kamopanorpa* (family Microptysmatidae) from the Chepanikha locality, Udmurtia; Urzhumian Stage, forewings: (a) *K. maculata* sp. nov., holotype PIN, no. 3286/80; (b) *K. tshepanikhensis* sp. nov., holotype PIN, no. 3286/76; (c) *Kamopanorpa* sp., specimen PIN, no. 3286/77. Scale bars, 1 mm.

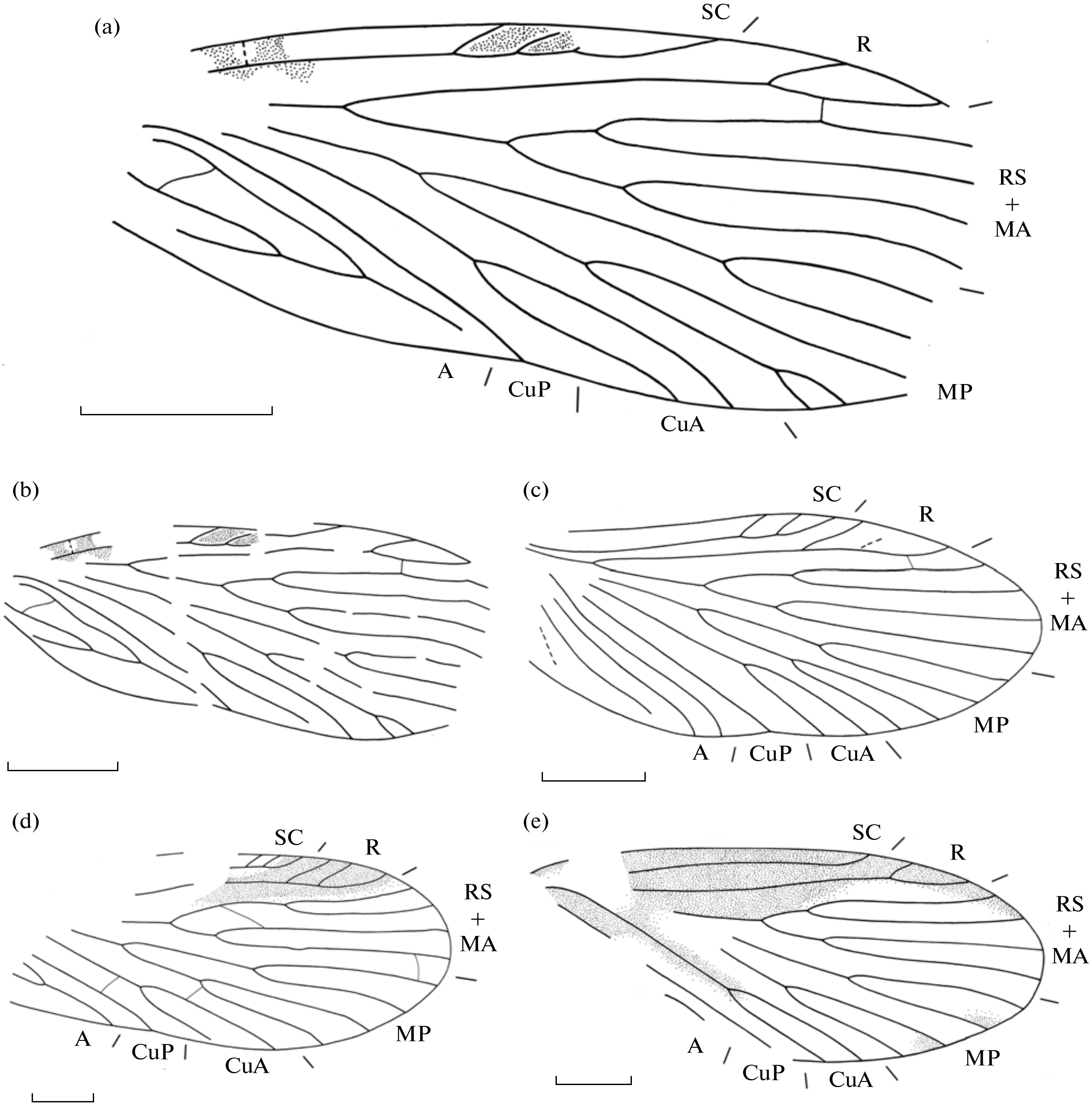

Fig. 68. New members of the families Cladochoristidae and Prorhyacophilidae: (a, b) *Cladochorista issadica* sp. nov., holotype PIN, no. 3840/192, forewing: (a) reconstruction and (b) preserved wing; (c) *?Cladochorista issadica* sp. nov., specimen PIN, no. 3840/1284, hindwing; Isady locality, Vologda Region; Severodvinian Stage; (d) *Cladochoristella ryzhkovae* sp. nov., holotype PIN, no. 5103/278, forewing; (e) *Prorhyacophila rasnitsyni* sp. nov., holotype PIN, no. 5103/206; Balymotikha locality, Vladimir Region; Vyatkian Stage. Scale bars, 1 mm.

and Upper Permian, these families coexisted with Protomeropidae and Microptysmatidae. Of five families of the suborder, only Cladochoristidae and Prorhyacophilidae cross the Paleozoic–Mesozoic boundary (Sukatsheva, 1973), whereas Protomeropidae and Microptysmatidae became extinct in the Upper Permian, and Uraloptysmatidae are endemic to the Lower Permian Chekarda locality.

Order Trichoptera Kirby, 1813

Suborder Protomeropina Tillyard, 1926

Family Microptysmatidae O. Martynova, 1958

Genus *Kamopanorpa* Martynov, 1928

Kamopanorpa maculata Sukatsheva et Aristov, sp. nov.

Etymology. Feminine gender form of the Latin *maculatus* (spotted).

Table 1. Geological and geographic distribution of caddisflies of the families Microptismatidae, Uraloptismatidae, Cladochoristidae, and Prorhyacophilidae. References: [1] Kukalová and Willmann (1990); [2] Novokshonov (1993); [3] Martynov (1933); [4] Ivanov (1992a); [5] Tillyard (1926); [6] Riek (1953); [7] Dijk and Geertsema (1999); [8] Sukacheva (1973); [9] Riek (1955); [10] Sukacheva (1982); [12] Martynova (1958)

Family	Genus	Species	Geological age	Locality
Microptismatidae O. Martynova, 1958	Microptismella Kukalová et Willmann, 1990	M. moravica Kukalová et Willmann, 1990	Lower Permian, Sakmarian Stage	Obora, Moravia, Czech Republic
	Kamopanorpa Martynov, 1928 (=Microptismodes O. Martynova, 1958 =Microptisma O. Martynova, 1958; Novokshonov, 1993)	K. lata Martynov 1928; =M. uralicus O. Martynova, 1958; Novokshonov, 1993	Middle Permian, Kazanian Stage	Tikhie Gory, Tatarstan, Russia
		K. uralensis Martynov, 1940; =K. fasciipennis O. Martynova, 1942; =K. pallida Sukatsheva, 1976; =K. incerta Sukatsheva, 1976; Novokshonov, 1993	Lower Permian, Urzhumian Stage	Chekarda, Perm Region, Russia
		K. rotundipennis Martynov, 1933	Middle Permian, Kazanian Stage	Soyana, Arkhangelsk Region, Russia
		K. sibirica (O. Martynova, 1958); Novokshonov, 1993	Middle Permian, Kazanian Stage	Sarbala, Kemerovo Region, Russia
		K. grossa Novokshonov, 1993	Middle Permian, Urzhumian Stage	Kostovaty, Udmurtia, Russia
		K. maculata sp. nov.	Middle Permian, Urzhumian Stage	Chepanikha and Kostovaty, Udmurtia, Russia
		K. mongolica (Sukatsheva, 1992).	Upper Permian, Severodvinian Stage	Bor-Tologoi, South Gobi Province, Mongolia
		K. sukatchevae Novokshonov, 1993	Upper Permian, Severodvinian Stage	Bor-Tologoi, South Gobi Province, Mongolia
		K. pritykinae (Sukatsheva, 1976); Novokshonov, 1993	Upper Permian, Vyatkian Stage	Karaungir, East Kazakhstan Province, Kazakhstan

Table 1. (Contd.)

Family	Genus	Species	Geological age	Locality
Microptismatidae O. Martynova, 1958	Kamopanorpa Martynov, 1928	K. latipennata Novokshonov, 1993	Upper Permian, Severodvinian Stage	Karaungir, East Kazakhstan Province, Kazakhstan
		K. karaungirica Novokshonov, 1993	Upper Permian, Severodvinian Stage	Karaungir, East Kazakhstan Province, Kazakhstan
		K. tshepanikhensis sp. nov.	Middle Permian, Urzhumian Stage	Chepanikha, Udmurtia, Russia
Uraloptismatidae Ivanov, 1992	Uraloptisma Ivanov, 1992	U. maculata Ivanov, 1992	Lower Permian, Kungurian Stage	Chekarda, Perm Region, Russia
Cladochoristidae Riek, 1953	Cladochorista Tillyard, 1926	C. belmontensis Tillyard, 1926	Upper Permian, Vyatkian Stage	Belmont, New South Wales, Australia
		C. sp.; Riek, 1953.	Upper Permian, Vyatkian Stage	Belmont, New South Wales, Australia
		C. issadica sp. nov.	Upper Permian, Severodvinian Stage	Isady, Vologda Region, Russia
		C. sp.; Dijk et Geerstsema, 1999	Upper Permian, Vyatkian Stage	Mooi River, Natal, South Africa
		C. multivenosa Sukatsheva, 1973	Middle Triassic, Ladinian Stage	Madygen, Osh Province, Kyrgyzstan
	Cladochoristella Riek, 1955	C. briani Riek, 1955	Upper Triassic, Carnian Stage	Ipswich, Queensland, Australia
		C. ryzhkovae sp. nov.	Upper Permian, Vyatkian Stage	Balymotikha, Vladimir Region, Russia
Prorhyacophilidae Riek, 1955	Prorhyacophila Riek, 1955 = Eocorona Tindal, 1980; Sukatsheva, 1982	P. colliveri Riek, 1955	Upper Triassic, Carnian Stage	Ipswich, Queensland, Australia
		P. rasnitsyni sp. nov.	Upper Permian, Vyatkian Stage	Vyazniki, Vladimir Region, Russia
		P. furcata Sukatsheva, 1973	Middle Triassic, Ladinian Stage	Madygen, Osh Province, Kyrgyzstan
		P. iani (Tindal, 1980); Sukatsheva, 1982	Upper Triassic, Carnian Stage	Ipswich, Queensland, Australia

Holotype. PIN, no. 3286/80, part and counterpart of forewing, well preserved; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 67a, 69a–69c). The forewing is rather broad, 2.6 times longer than wide. The widest point is at the level of the first bifurcation of the distal branch of MP. The anterior wing margin is weakly convex; the wing apex is rounded. SC is long, ending somewhat proximal to the base of the bifurcation in R and distal to the bifurcation in F_1. The costal space is rather narrow, its basal one-third is half as wide as the subcostal space, and crossed by four crossveins: the straight 1c-sc at the very base of the wing and three almost straight veins in the basal one-third of the wing. The subcostal space is wide, crossed by four crossveins: the weakly convex oblique 1sc-r located distal to the point of divergence of RS and R, two oblique veins (2sc-r, 3sc-r) in the basal half of the wing, and short oblique 4sc-r located proximal to the apex of SC. R is straight, long, with a short, wide bifurcation at the end; RS diverges from R slightly proximal to the distal boundary of the basal quarter of the wing; RS + MA has six branches. The stem RS_{1+2} is twice as long as the stem MA. The bifurcation of F_1 is 1.3 times as long as the bifurcation of F_2. F_3 is six times as long as its stem. The cells DC, MC, and TC are open. MP has six branches, branching somewhat distal to the bifurcation RS + MA and proximal to the middle of the wing length. The bifurcations in MP_1, MP_3, and CuA are almost equal in length; MP_2 and MP_4 are simple. A long, weakly curved MP_5 is present. The Y-shaped vein has unequal arms. CuP is short, simple, reaches the posterior wing margin separately from A_1. A_2 is long, 1.7 times as long as A_3. The crossvein a_1–a_2 is present. The anal space is of moderately wide. The wing membrane is dark. The coloration pattern is distinct, composed of light spots varying in size and becoming more intense towards the wing base and apex. A large light rounded spot is in the middle of the wing.

Measurements, mm. Forewing length, 7.0; width, 3.0.

Comparison. The new species is most similar in size and the presence of six-branched MP to *K. grossa* Novokshonov, 1993 from the Kostovaty locality and to *K. tshepanikhensis* sp. nov. from the Chepanikha locality. *K. maculata* sp. nov. differs from *K. grossa* in the greater number of crossveins in the costal and subcostal spaces and in the presence of the vein a_1–a_2. *K. grossa* has only one crossvein in the costal space and the vein a_1–a_2 is absent (Novokshonov, 1993). The new species differs from *K. tshepanikhensis* in the coloration pattern (the large rounded light spot in the middle of the wing) and in the open cell DC. It differs from all other congeners, except *K. grossa,* in the three branches of the basal branch of MP. In the other species of the genus, except *K. grossa,* the basal branch of MP has two branches or is simple (Martynov, 1933; Sukatsheva, 1976; Novokshonov, 1993).

Remarks. The coloration pattern in the form of spots occurs in some other species of the genus, e.g., *K. uralensis* (Martynov, 1940; Novokshonov, 1992).

Material. In addition to the holotype, specimen PIN, no. 3695/15 (Fig. 69c) from the Kostovaty locality, Udmurtia, Urzhumian Stage, not included in the type series.

Kamopanorpa tshepanikhensis Sukatsheva et Aristov, sp. nov.

Etymology. From the Chepanikha locality.

Holotype. PIN, no. 3286/76, part and counterpart of incomplete forewing; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 67b, 69d, 69e). The forewing is rather broad, thrice longer than wide. The anterior wing margin is weakly convex; the wing apex is pointed, located between the bifurcations of F_2 and F_3. SC is long, ending at the level of the base of the bifurcation of R. The costal space is wide in the basal part, becoming narrower distally, where it is 0.59 as wide as the subcostal space. The costal space is crossed by four crossveins: strong straight 1c-sc at the wing base, two oblique veins 2sc-r and 3sc-r proximal to the middle of the wing length, and 4sc-r near the apex of SC. The subcostal space lacks crossveins, almost as wide as the costal space. R is straight, with a rather narrow terminal bifurcation. RS + MA has six branches, diverges from R at the level of the distal boundary of the basal quarter of the wing. The stem of MA is very short; the stem RS is 3.6 longer than the stem of MA. The bifurcations of F_1 and F_2 are subequal in length; the bifurcation of F_3 is very long, 11.4 as long as its stem. The cell DC is closed by a weak crossvein located at the level of the base of the bifurcation of the distal branch of MP. RS + MA and MP diverge almost at the same level, proximal to the middle of the wing length; M_5 is long, curved; the Y-shaped vein has strongly unequal arms. A_2 is 1.7 times longer than A_3; the anal space is narrow. The wing membrane is dark; the coloration pattern is composed of light spots on the dark membrane, becoming more intense in the middle and at the base of the wing.

Measurements, mm. Forewing length, 8.0; width, about 3.0.

Comparison. The new species is particularly similar in venation (six branches of MP) and size of the forewing to *K. grossa* from the Kostovaty locality and *K. maculata* sp. nov. from the Kostovaty and Chepanikha localities. *K. tshepanikhensis* differs from *K. grossa* in the greater number of crossveins in the costal space and in the presence of the vein a_1–a_2. *K. grossa* has only one crossvein in the costal space and veins in the subcostal space and the vein a_1–a_2, are absent (Novokshonov, 1993). *K. tshepanikhensis* differs from *K. maculata* in the coloration pattern (large light rounded

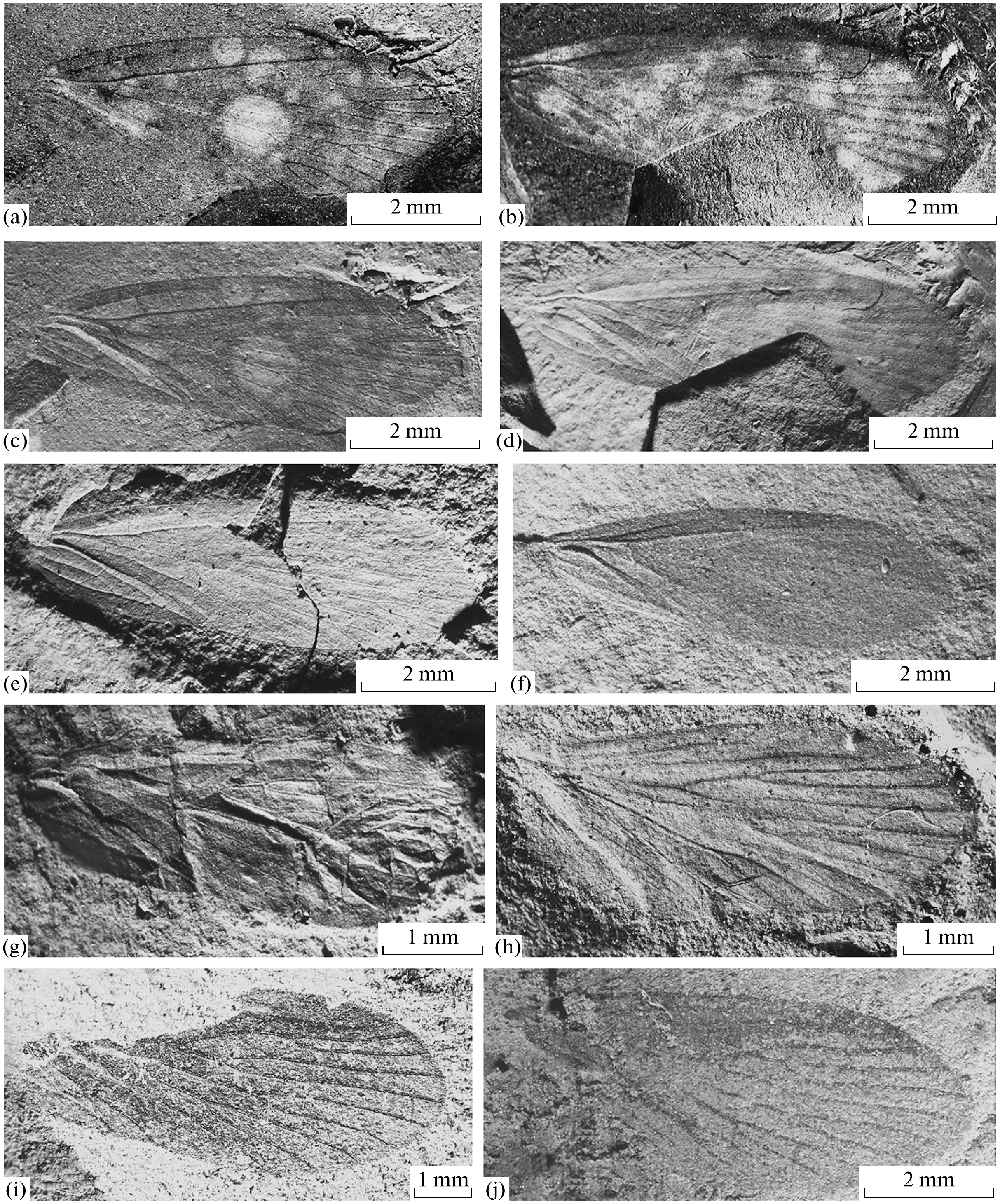

Fig. 69. New members of the suborder Protomeropina: (a–c) *Kamopanorpa maculata* sp. nov.: (a, b) holotype PIN, no. 3286/80, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage: (a) more contrast photograph; (b) less contrast photograph; (c) specimen PIN, no. 3695/15, forewing; Kostovaty locality, Udmurtia; Urzhumian Stage; (d, e) *Kamopanorpa tshepanikhensis* sp. nov., holotype PIN, no. 3286/76, forewing: (d) more contrast photograph; (e) less contrast photograph; (f) *Kamopanorpa* sp., specimen PIN, no. 3286/77, forewing; Chepanikha locality, Udmurtia; Urzhumian Stage; (g) *Cladochorista issadica* sp. nov., holotype PIN, no. 3840/192, forewing; (h) *?Cladochorista issadica* sp. nov., specimen PIN, no. 3840/1284, hindwing; Isady locality, Vologda Region; Severodvinian Stage; (i) *Cladochoristella ryzhkovae* sp. nov., holotype PIN, no. 5103/278, forewing; (i) *Prorhyacophila rasnitsyni* sp. nov., holotype PIN, no. 5103/206, forewing; Balymotikha locality, Vladimir Region; Vyatkian Stage.

spot in the middle of the wing is absent) and in the closed cell DC.

Material. Holotype.

Family Cladochoristidae Riek, 1953

Genus *Cladochorista* Tillyard, 1926

Cladochorista issadica Sukatsheva et Aristov, sp. nov.

Etymology. From the Isady locality.

Holotype. PIN, no. 3840/192, direct impression of slightly distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 68a, 68b, 69g). The forewing is rather broad, 2.3 times longer than wide. The greatest width of the wing is at the level of the apex of CuA_1. The anterior wing margin is weakly convex. SC is rather short, with three or more branches, ending proximal to the base of the bifurcation of the basal branch of MP. At the wing base, the subcostal space is half as wide as the costal space. R is straight, with a wide, large terminal bifurcation. There is a crossvein between R and RS_1 in the apical part of the wing. RS + MA has four branches. The stem RS + MA is 1.5 times as long as the stem RS_1 and 1.6 times as long as the stem MA. The stem MA is 1.4 times longer than the stem RS_1. The cells DC and MC are open. The apex of the bifurcation of MP is located considerably proximal to the apex of the bifurcation RS + MA. MP has five branches; the distal branch of MP has a of moderately long bifurcation; the basal branch has a long bifurcation and a very short terminal bifurcation of MP_3. CuA has a long bifurcation. CuP is short, reaches the posterior wing margin separately from A_1. Coloration pattern is present, composed of rather small dark spots between the veins in the costal space and at the base of SC.

Measurements, mm. Forewing length, 4.5; width, 1.8.

Comparison. The new species differs from *C. belmontensis* Tillyard, 1926 from the Upper Permian of Australia and *C. multivenosa* Sukatsheva, 1973 from the Middle Triassic of Kyrgyzstan in the bifurcation of R and in the stems of bifurcations in the distal and basal branches of MP strongly differing in length. The new species is most similar to *Cladochorista* sp. from the Upper Permian (Prevec et al., 2009) Mooi River locality (Pl. 1) and differs from it in the smaller number of branches of SC and in the considerably narrower costal space. In this *Cladochorista* sp., SC has more than seven branches and the costal space at the wing base is only 1.3 as wide as the subcostal space (Dijk and Geerstsema, 1999).

Material. Holotype.

?Cladochorista issadica Sukatsheva et Aristov, sp. nov.

Description (Figs. 68c, 69h). The hindwing is wide, 2.3 as long as wide. The greatest width of the wing is at the level of the apex of CuA_2, at the point where it reaches the posterior wing margin. The anterior wing margin is weakly convex. SC is rather short, with two branches, ending at the level of the point where the branch CuA_2 reaches the posterior wing margin . The subcostal space is constant in width over the entire extent. R is straight, with a weak apical curve and wide terminal bifurcation. The apical part of the wing has a slightly oblique crossvein between R and RS_1. RS + MA has four branches. The stem RS + MA is 1.2 as long as the stem RS_1 and 1.3 as long as the stem MA. The stem RS_1 is 1.1 as long as the stem RS_2. The cells DC and MC are open. The apices of the bifurcations of RS + MA and MP are at the same level. MP has four branches, with bifurcations equal in length. CuA has a long bifurcation. CuP and anal veins are long, simple, running parallel to each other in the weakly dilated anal area. An anojugal fan is absent.

Measurements, mm. Hindwing length, 5.0; width, 2.2.

Remarks. This specimen from the Isady locality probably represents the only presently known hindwing of Cladochoristidae. The general pattern of its venation, some features of the systems RS + MA and MP and size resemble the forewing of *Cladochorista issadica* sp. nov. Based on this similarity and the homonomy of the hindwing and forewing characteristic of primitive Trichoptera, this hindwing is provisionally attributed to *C. issadica*.

Interestingly, in the Early Permian Microptismatidae, all anal veins of the hindwing reach the posterior wing margin independently. The hindwing of Late Permian Microptismatidae and Protomeropidae already has a structure similar to the anal loop, like the forewing (Novokshonov, 1997). The cladochoristid hindwing found in Isady lacks a trace of the formation of the anal loop.

Material. Specimen PIN, no. 3840/1284, part and counterpart of hindwing; Isady locality, Vologda Region; Severodvinian Stage.

Genus *Cladochoristella* Riek, 1955

Cladochoristella ryzhkovae Sukatsheva et Aristov, sp. nov.

Etymology. In honor of the paleoentomologist O.V. Ryzhkova.

Holotype. PIN, no. 5103/278, part and counterpart of well-preserved incomplete forewing; Balymotikha locality, Vladimir Region; Vyatkian Stage.

Description (Figs. 68d, 69i). The forewing is wide, 2.7 as long as wide. The pterostigma is clearly pronounced. The wing apex is rounded, located opposite the end of MA_2. SC is long, with two branches near the apex, reaches the anterior wing margin slightly distal to the base of the second branch of R. R is arcuate in the apical part, with two parallel branches near the apex. RS + MA has four branches and long, narrow bifurcations. The cell DC is closed by a strongly oblique crossvein, which diverges anteriad from the middle of the stem RS_{1+2}. The stem RS_{1+2} is approximately 2.5 times as long as the stem MA. The cell MC is open. In the apical part of the wing, between MA_2 and MP_1, there is a straight, strong crossvein. The apex of the bifurcation of MP is somewhat proximal to the apex of the bifurcation RS + MA. MP has four branches. The stem M_{1+2} is 1.5 times as long as the stem M_{3+4}. CuA has a long bifurcation. Between MP_4 and CuA_1, distal to the apex of F_4, there is a short oblique crossvein. CuP is short, reaches the posterior wing margin at a large distance from short A_1. The wing membrane is generally dark, somewhat lighter near the wing apex and darker in the pterostigma area.

Measurements, mm. Forewing length, about 9; width, 3.5.

Comparison. The new species is similar to the type species of the genus, *C. briani* Riek, 1955 from the Upper Triassic of Australia, in the presence of two subapical branches of R and in the type of the crossvein MP_4—cua_1 (Riek, 1955); the new species differs from the type species in the long SC with two subapical branches, very long stem RS_{1+2}, and in the somewhat larger size.

Material. Holotype.

Family Prorhyacophilidae Riek, 1955

Genus *Prorhyacophila* Riek, 1955

Prorhyacophila rasnitsyni Sukatsheva et Aristov, sp. nov.

Etymology. In honor of the paleoentomologist A.P. Rasnitsyn.

Holotype. PIN, no. 5103/206, direct impression of poorly preserved incomplete forewing; Balymotikha locality, Vladimir Region; Vyatkian Stage.

Description (Figs. 68e, 69j). The forewing is broad, 2.5 times longer than wide. The greatest wing width is at the level of the base of the bifurcation of MA. The anterior wing margin is weakly convex; the apex is rounded, located opposite the end of MA_2. SC is long, simple, reaches the anterior wing margin somewhat proximal to the apex of the bifurcation of R. R is weakly arcuate, with a wide terminal bifurcation. RS + MA has four branches and long, narrow bifurcations. The stem MA is 1.4 times as long as the stem RS_{1+2}. MP also has four branches; its bifurcations are rather long, moderately long. F_3 begins distal to F_4 and is 1.1 as long as F_4. The cells DC, MC, and TC are open. The Y-shaped vein has arms of unequal length.

Measurements, mm. Forewing length, 7.5; forewing width, 3.5.

Comparison. In the location of the bifurcations of RS + MA and MP, the new species is most similar to *P. furcata* Sukatsheva, 1973 and differs from it and all known species of *Prorhyacophyla* in the simple SC. In other species of *Prorhyacophyla,* SC has a bifurcation (Sukatsheva, 1973).

Material. Holotype.

2.6. New Grylloblattids (Insecta: Grylloblattida) from the Upper Permian of the Vologda Region

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In this chapter, new Grylloblattida (Insecta) from the Upper Permian Isady locality (Severodvinian Stage of the Vologda Region) are described, including *Chauliodites circumornatus* sp. nov., *C. geniatus* sp. nov., *Purtovinia ustyugensis* gen. et sp. nov., *Permyak involucris* gen. et sp. nov. (Chauliodititidae), *Geinitzia subita* sp. nov., *Shurabia permiana* sp. nov., *Sukhonia coriacea* gen. et sp. nov. (Geinitziidae), *Sylvaella semicolorata* sp. nov., *Liomofrater circumcisus* gen. et sp. nov., *Falseshurabia transitoria* gen. et sp. nov. (Liomopteridae), *Mesoidelia gorochovi* sp. nov. (Mesorthopteridae), *Parakhosara reticulata* sp. nov., *Abbrevikhosara ovoidea* gen. et sp. nov. (Megakhosaridae), *Baharellinus porrectus* sp. nov. (Blattogryllidae), *Issadonympha oculea* gen. et sp. nov., and *Kenguronympha lenta* gen. et sp. nov. (Grylloblattida incertae sedis). *Chauliodites issadensis* Aristov, 2009 (Chauliodititidae) is redescribed.

Grylloblattids are the most diverse group of insects in Isady. The order is represented by 11 families, 24 genera, and 30 species, which make up about 9% of all insect specimens identifiable to order. During the period from 2005 to 2010, a total of more than 200 grylloblattid specimens were collected in Isady; 87 of them have been identified to family. The dominant family is Chauliodititidae, which makes up 30% of grylloblattids and includes three genera and seven species. Somewhat less abundant are the families Megakhosaridae (four genera, six species) and Geinitziidae (three genera with three species), which make up 22% each. The families Liomopteridae (three genera and species) and Blattogryllidae (one genus with two species) make up 9 and 3%, respectively. Members of the families Mesorthopteridae, Permotermopsidae, Cacurgidae, Tunguskapteridae, Kortshakiliidae, and Permulidae are infrequent; each is represented by a single species. For a detailed discussion and the list of the grylloblattid fauna of the Isady locality, see Chapter 1.2.3.

Order Grylloblattida Walker, 1914

Suborder Grylloblattina Walker, 1914

Family Chauliodititidae Handlirsch, 1906

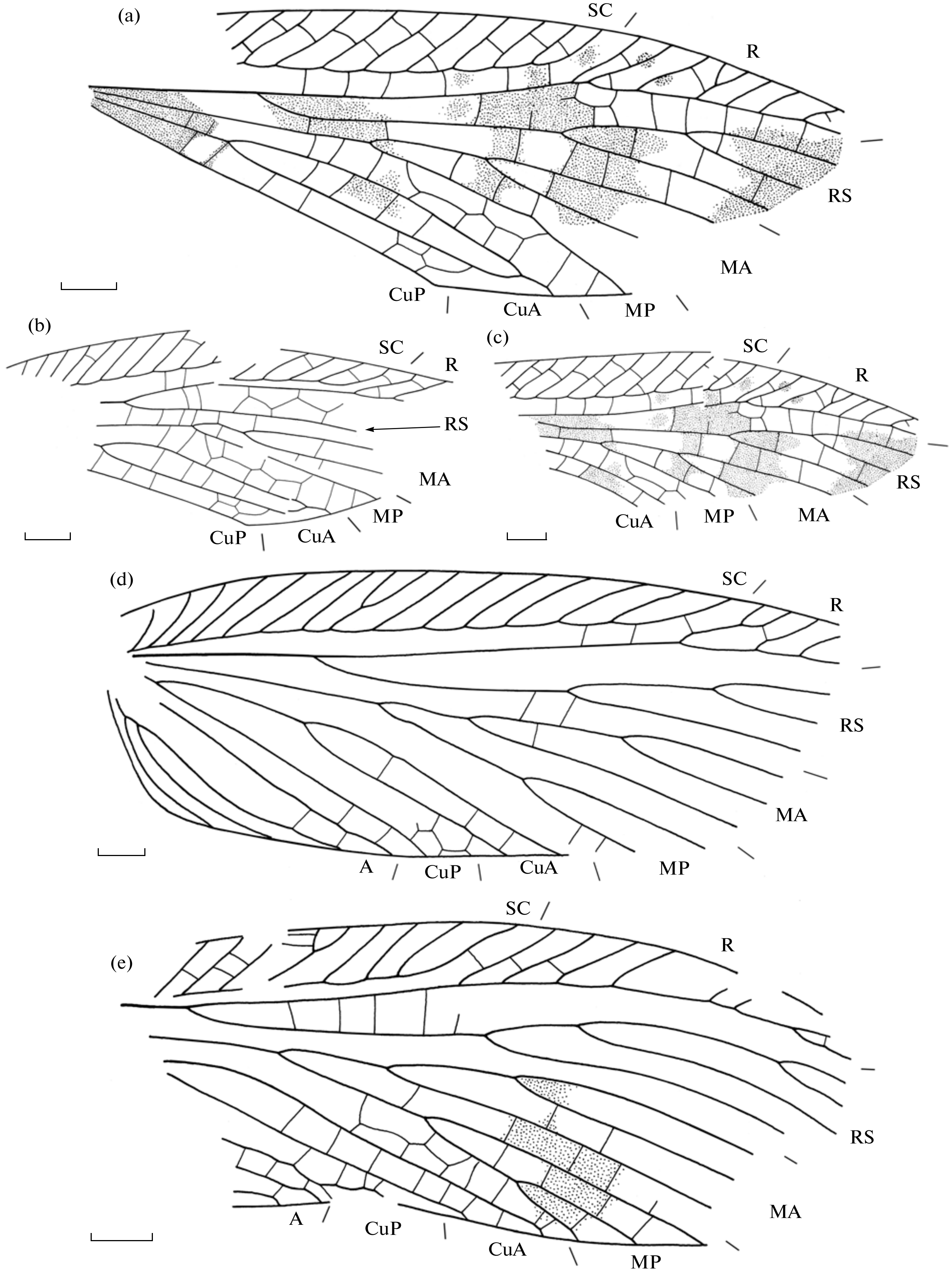
Genus *Chauliodites* Heer, 1864

Chauliodites issadensis Aristov, 2009

Chauliodites issadensis: Aristov, 2009c, p. 18, text-figs. 1 and 2.

Holotype. PIN, no. 3840/91, direct impression of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Redescription (Figs. 70a–70c, 72a, 72b). Medium-sized insect. The anterior forewing margin is


(a)
SC
R
RS
MA
CuP
CuA
MP
(b)
SC
R
RS
MA
MP
CuP
CuA
(c)
SC
R
RS
MA
MP
CuA
(d)
SC
R
RS
MA
MP
A
CuP
CuA
(e)
SC
R
RS
MA
MP
A
CuP
CuA

convex; the costal space at the base of RS is twice as wide as the subcostal space. SC has simple, straight, and slightly S-shaped anterior branches connected by crossveins; it ends in the distal one-third of the wing. The anterior branches of R are simple, S-shaped and Y-shaped. RS begins in the basal one-third of the wing and has three branches. M is divided into MA and MP in the basal one-third of the wing; MA has two branches; MP is simple, not desclerotized. CuA is straight proximal to the division into CuA_1 and CuA_2, which is in the basal one-third of the wing. The apex of CuA_2 is fused with CuA_1; both stems reach the posterior wing margin in one apex, with a sharp curve at the point of fusion with a crossvein. CuP is straight. Crossveins are simple, straight, forming a double row of cells in the interradial, medial, and intercubital spaces. The wing membrane has dark spots.

Measurements, mm. Forewing length, about 14.

Remarks. The material collected in 2009 and 2010 contains additional specimens of *C. issadensis*, which allows redescription of this species. In particular, it has been shown that SC ends in the distal one-third of the wing rather than near the apex. A sharp curve of the anterior wing margin distal to the apex of SC in the holotype was caused by deformation of the rock.

Material. In addition to the holotype, specimens PIN, nos. 3840/547, 1256 from the same locality.

Chauliodites geniatus Aristov, sp. nov.

Etymology. The Latin *geniatus* (beautiful).

Holotype. PIN, no. 3840/1255, direct impression of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 70d, 72c). Medium-sized insect. The anterior forewing margin is weakly convex. The costal space at the base of RS is thrice as wide as the subcostal space. SC ends in the distal one-third of the wing, distal to the apex of CuA_1. The anterior branches of SC and R are straight and slightly curved, simple and Y-shaped. RS begins at the distal boundary of the basal quarter of the wing and starts branching near the middle of its extent; it is pectinate and has three branches. M is divided into MA and MP at a small distance from the base of RS. MA branches proximal to the bifurcation of RS and has three branches; MP branches distal to the bifurcation of MA, but proximal to the bifurcation of RS and has two branches. CuA is divided into simple CuA_1 and CuA_2 at the level of the base of RS. The apex of CuP curves posteriad; A_1 is simple; A_2 has three branches. Crossveins are simple and form a double row of cells at the apex of the intercubital space.

Measurements, mm. Forewing length, about 19.

Comparison. The new species is most similar to *C. ramosus* (Aristov, 2003) from the Lower Triassic of the Kemerovo Region and *C. circumornatus* sp. nov. from Isady; it differs from both in the longer SC. In *C. ramosus* and *C. circumornatus,* SC ends near the middle of the wing, approximately at the level of the apex of CuA_1 (Aristov, 2003; see below).

Material. Holotype.

Chauliodites circumornatus Aristov, sp. nov.

Etymology. The Latin *circumornatus* (decorated).

Holotype. PIN, no. 3840/1258, direct impression of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 70e, 71a–71e, 72d–72g). Medium-sized insect. The anterior forewing margin is weakly convex. The costal space at the base of RS is 3.5 times as wide as the subcostal space. SC ends immediately distal to the middle of the wing, approximately at the level of the apex of CuA_1. The anterior branches of SC are straight, simple and Y-shaped, connected by crossveins. R reaches the wing apex and has simple, slightly curved anterior branches. RS begins in the basal quarter of the wing and starts branching near the middle of its own length; it is pectinate or dichotomous and has four branches. M is divided into MA and MP at a small distance from the base of RS. MA branches proximal to the bifurcation of RS and has three or four branches; MP branches distal to the bifurcation of MA, but proximal to the bifurcation of RS and has two or three branches. CuA is divided into simple CuA_1 and CuA_2 at the level of the base of RS. The apex of CuP curves towards CuA_2. Crossveins are simple, Y-shaped, and H-shaped and can form a double row of cells in the interradial, medial, and intercubital spaces. The coloration is in the form of shapeless spots in the middle and distal half of the wing.

Measurements, mm. Forewing length, about 15.

Comparison. The new species is most similar to *C. ramosus* (Aristov, 2003) from the Lower Triassic of the Kemerovo Region, from which it differs in the more distal bifurcation of RS and in the more proximal bifurcations of MA and MP. In *C. ramosus,* RS branches in its basal one-third, and MA and MP branch distal to the bifurcation of RS (Aristov, 2003).

←

Fig. 70. Members of the genus *Chauliodites* (Chauliodititidae) from the Isady locality, Vologda Region; Severodvinian Stage, forewings: (a–c) *Chauliodites issadensis* Aristov, 2009: (a) reconstruction based on holotype and specimens PIN, nos. 3840/547 and 1256; (b) specimen PIN, no. 3840/547; (c) specimen PIN, no. 3840/1256; (d) *C. geniatus* sp. nov., holotype PIN, no. 3840/1255; (e) *C. circumornatus* sp. nov., holotype PIN, no. 3840/1258. Scale bars, 1 mm.

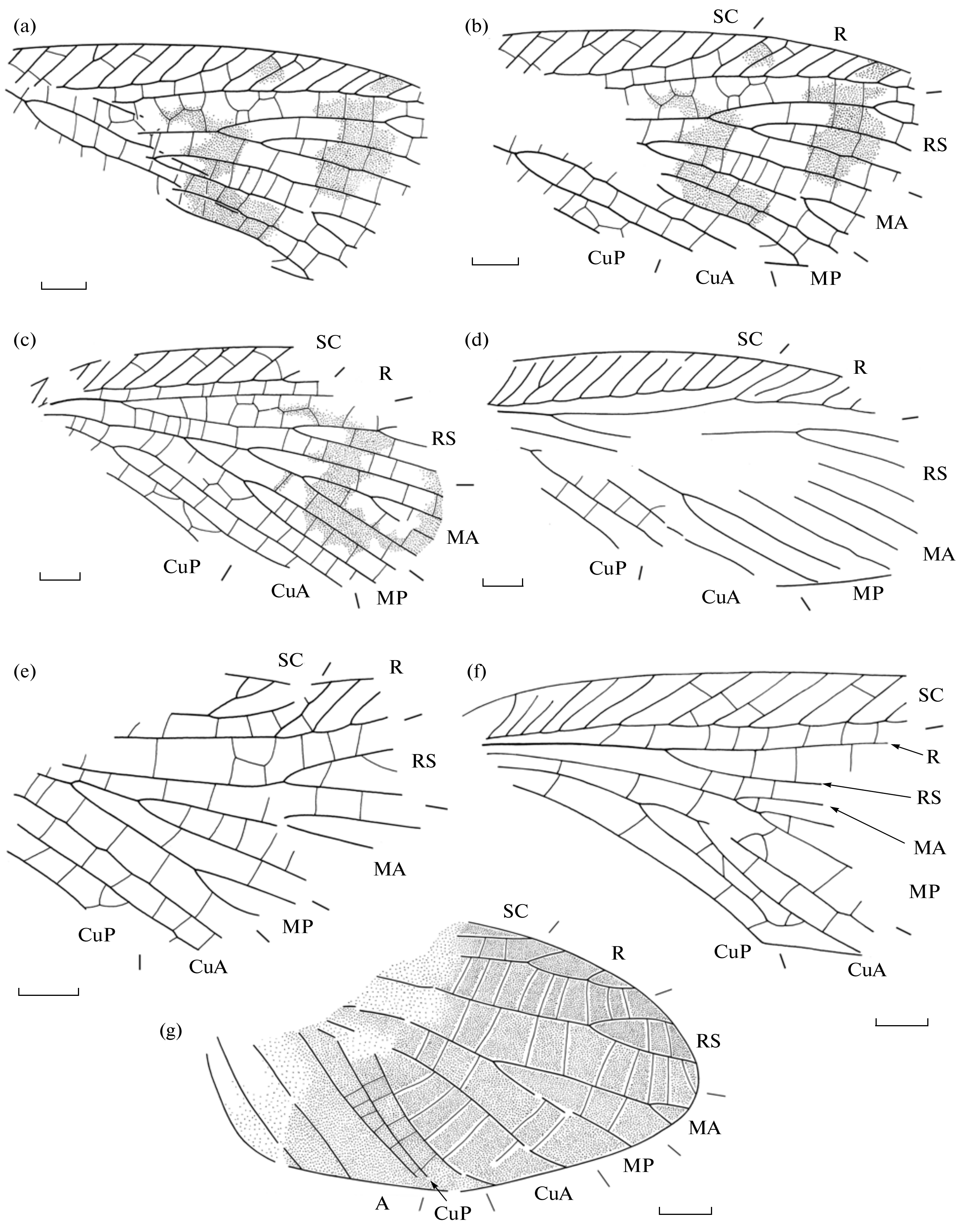


Fig. 71. Members of the family Chaulioditidae from the Isady locality, Vologda Region; Severodvinian Stage, forewings: (a–e) *Chauliodites circumornatus* sp. nov.: (a, b) paratype PIN, no. 3840/1260: (a) line drawing of impression; (b) reconstruction; (c) paratype PIN, no. 3840/1257; (d) paratype PIN, no. 3840/1259; (e) paratype PIN, no. 3840/1262; (f) *Purtovinia ustyugensis* sp. nov., holotype PIN, no. 3840/543; (g) *Permyak involucris* sp. nov., holotype PIN, no. 3840/2091. Scale bars, 1 mm.

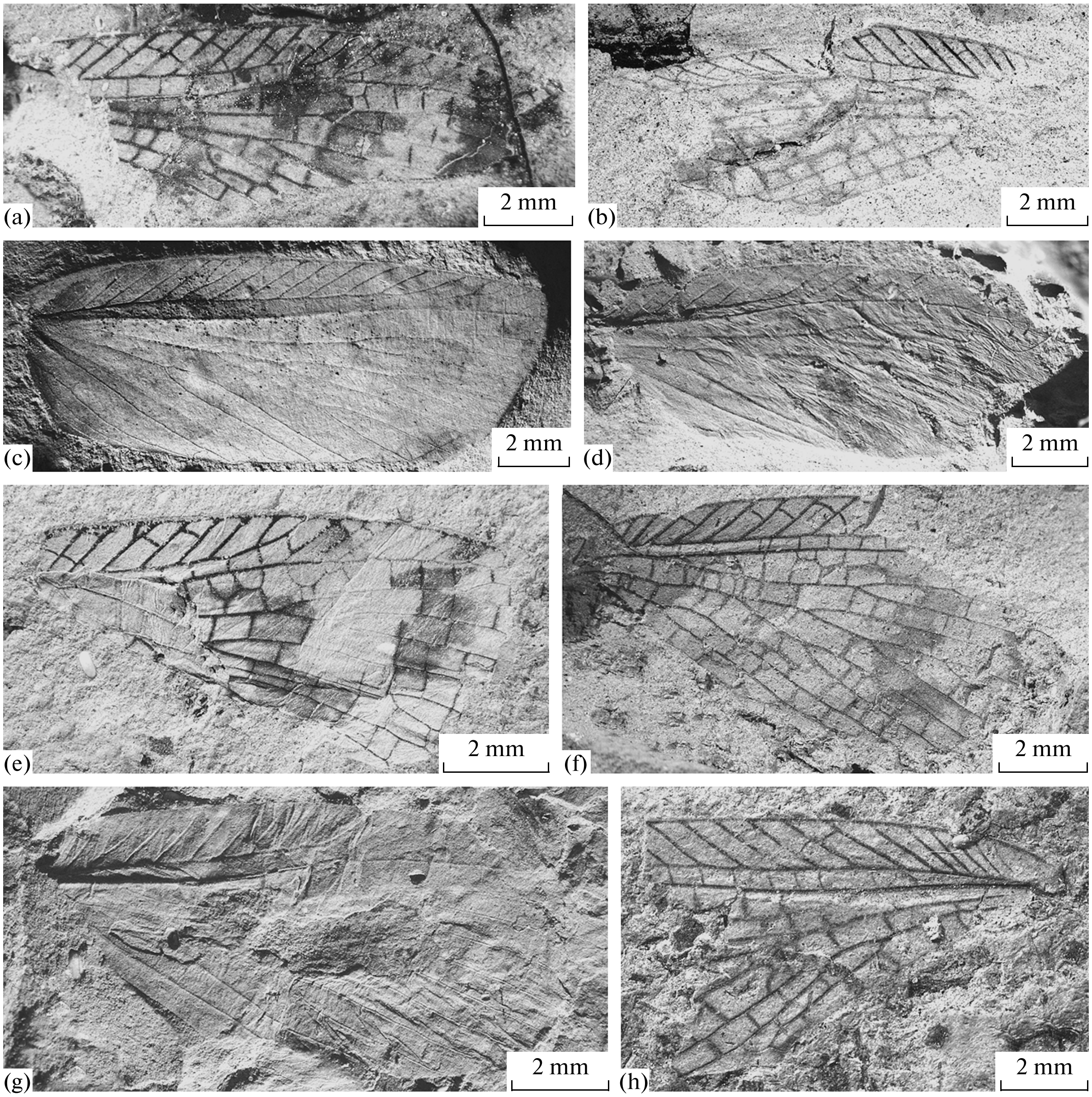


Fig. 72. Members of the family Chauliodititidae from the Isady locality, Vologda Region; Severodvinian Stage, forewings: (a, b) *Chauliodites issadensis* Aristov, 2009: (a) specimen PIN, no. 3840/1256; (b) specimen PIN, no. 3840/547; (c) *C. geniatus* sp. nov., holotype PIN, no. 3840/1255; (d–g) *C. circumornatus* sp. nov.: (d) holotype PIN, no. 3840/1258; (e) paratype PIN, no. 3840/1260; (f) paratype PIN, no. 3840/1257; (g) paratype PIN, no. 3840/1259; (h) *Purtovinia ustyugensis* sp. nov., holotype PIN, no. 3840/543.

C. circumornatus is also similar to *C. geniatus* from Isady, from which it differs in the shorter SC. In *C. geniatus,* SC ends in the distal one-third of the wing, distal to the apex of CuA_1 (see above).

Material. In addition to the holotype, paratypes PIN, nos. 3840/1257, 1259, 1260, 1262 from the same locality.

Genus *Purtovinia* Aristov, gen. nov.

Etymology. From the village of Purtovino near the locality. Gender feminine.

Type species. *P. ustyugensis* sp. nov.

Diagnosis. Medium-sized insect. In forewing, costal space at base of RS twice as wide as subcostal space. RS beginning in basal quarter of wing. M branching distal to base of RS before middle of wing; MP starting branching at base. CuA_1 with two branches; CuA_2 not reaching posterior wing margin.

Species composition. Type species.

Comparison. In the shape of M, branching distal to the base of RS, and in the early branching CuA_1, the new genus is most similar to *Miralioma*

Aristov, 2004 from the Upper Kazanian of the Kirov Region and the Urzhumian of Udmurtia and differs from which it in the proximally branching M. In *Miralioma,* M branches near the middle of the wing (Aristov, 2004e; Aristov and Bashkuev, 2008).

Remarks. The genus *Miralioma* was described in the family Liomopteridae (Aristov, 2004e) and subsequently transferred to Chaulioditidae based on the presence of the distally branching M (Aristov et al., 2009a).

Purtovinia ustyugensis Aristov, sp. nov.

Etymology. From the city of Velikii Ustyug.

Holotype. PIN, no. 3840/543, impression of distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 71f, 72h). The anterior wing margin is straight. SC ends in the distal half of the wing and has simple, straight, and slightly S-shaped anterior branches, connected with crossveins. R is S-shaped distal to the point where RS diverges from it. CuA is divided into CuA_1 and CuA_2 at the level of the base of RS; CuA_1 branches in its basal quarter; CuA_2 ends into two crossveins near the posterior wing margin. Crossveins are simple and Y-shaped in the medial space.

Measurements, mm. Forewing length, about 16.

Material. Holotype.

Genus *Permyak* Aristov, gen. nov.

Etymology. From the Permian period. Gender masculine

Type species. *P. involucris* sp. nov.

Diagnosis. Medium-sized insect. Brachypterous forewing twice longer than wide. Costal space smoothly narrowing at apex of SC. SC ending proximal to distal one-third of wing. R reaching anterior wing margin. RS beginning proximal to middle of wing, with branches reaching anterior margin and apex of wing. M divided into MA and MP distal to middle of wing. CuA_1 simple; CuP ending proximal to middle of wing.

Species composition. Type species.

Comparison. The new genus differs from other members of the family in the wing proportions and in the anterior branch of RS reaching the anterior wing margin. In the other Chaulioditidae, the anterior branch of RS reaches the wing apex and other brachypterous forms are not known (Aristov, 2003, 2004e, 2005; 2008a; 2009a).

Remarks. Anterior branches of RS, which reaches the anterior wing margin, are characteristic of the family Geinitziidae. However, in this case, these characters could have emerged as a result of wing shortening. Therefore, based on the presence of the distally branching M in combination with simple CuA_1, *P. involucris* is assigned here to Chaulioditidae. The wing proportions and reduction of venation suggest that the wing of *P. involucris* was probably brachypterous. Such wings are shortened by at most one-half and do not lose the original venation pattern, in contrast to micropterous wings (Sinitshenkova, 1987). *P. involucris* is the only brachypterous chaulioditid described to date. The brachyptery is a rather rare phenomenon among grylloblattids and, apart from Chauloditidae, it is known in one member of each of the families Liomopteridae (Aristov et al., 2009a), Blattogryllidae (Aristov, 2011a), and Megakhosaridae (see below). It is noteworthy that three of four brachypterous grylloblattids are known from the Upper Permian.

Permyak involucris Aristov, sp. nov.

Etymology. The Latin *involucris* (flightless).

Holotype. PIN, no. 3840/2091, part and counterpart of incomplete brachypterous forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 71g, 75a). R has two anterior branches; RS branches in the distal quarter of the wing and has two ends. MA has one short bifurcation; MP is simple. The intercubital space is narrower than the space between CuA_1 and CuA_2. A_1 is simple; A_2 has two branches. Crossveins are simple. The wing membrane is dark, with light stripes along the veins.

Measurements, mm. Forewing length, about 11; width, about 5.5.

Material. Holotype.

Family Geinitziidae Handlirsch, 1906

Genus *Geinitzia* Handlirsch, 1906

Geinitzia subita Aristov, sp. nov.

Etymology. From the Latin *subita* (unexpected).

Holotype. PIN, no. 3840/1239, part and counterpart of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 73a, 75b). The anterior forewing margin is straight. The costal space at the base of RS is equal in width to the subcostal space. SC has densely spaced, simple anterior branches and ends near the middle of the wing. R ends proximal to the distal one-third of the wing. RS begins in the basal quarter of the wing; it is pectinate posteriad, with three or more branches. The interradial space is dilated, equal in width to the preradial space. M is divided into branches proximal to the base of RS; MA and MP have two or more ends each. CuA_1 branches near the middle and ends in the distal one-third of the wing in three branches. The apex of CuA_2 is S-shaped. Crossveins are simple; in the interradial space, they are long, S-shaped.

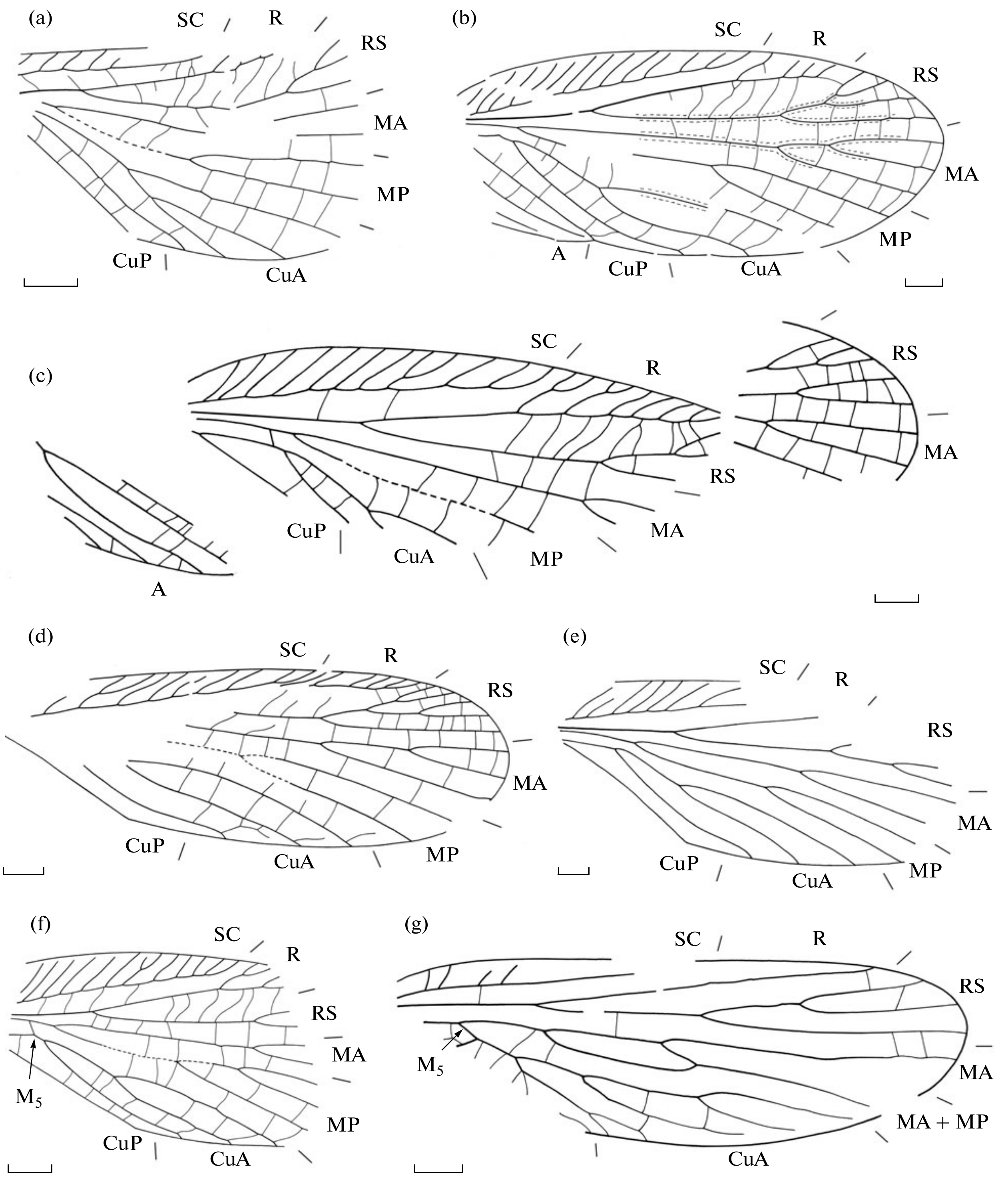


Fig. 73. Members of the family Geinitziidae from the Isady locality, Vologda Region; Severodvinian Stage, forewings: (a) *Geinitzia subita* sp. nov., holotype PIN, no. 3840/1239; (b–f) *Shurabia permiana* sp. nov.: (b) holotype PIN, no. 3840/3101; (c) paratype PIN, no. 3840/549 (three fragments of one wing preserved close to each other); (d) paratype PIN, no. 3840/1237; (e) paratype PIN, no. 3840/548; (f) paratype PIN, no. 3840/1242; (g) *Sukhonia coriacea* sp. nov., holotype PIN, no. 3840/796. Scale bars, 1 mm.

Measurements, mm. Forewing length, about 9.5.

Comparison. The new genus differs from congeners in the narrow costal space and in the dilated interradial space. In the other species of *Geinitzia,* the costal space at the base of RS is wider than the subcostal space, and the interradial space is narrower than the preradial space (Storozhenko, 1998; Aristov et al., 2009b).

Material. Holotype.

Genus *Shurabia* Martynov, 1937

Shurabia permiana Aristov, sp. nov.

Etymology. From the Permian period.

Holotype. PIN, no. 3840/3101, part and counterpart of distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 73b–73f, 75c–75g). Medium-sized insect. The anterior forewing margin is convex; the apex is weakly pointed. The costal space at the base of RS is 1.5 as wide as the subcostal space. SC has 8–13 simple and Y-shaped anterior branches and ends proximal to the distal quarter of the wing. RS begins in the basal one-third of the wing; in the distal one-third of the wing, it forms a posterior comb of branches or is divided irregularly. RS has from four to six branches reaching the anterior margin and apex of the wing. M_5 is well pronounced; M is divided into MA and MP at the level of the first bifurcation of CuA or somewhat more distally. MA and MP start branching near the middle of the wing or in its distal one-third; MA and MP have two or three branches each. CuA_1 is divided into two branches in the basal quarter or one-third of its extent; the apex of CuA_2 is S-shaped. The apices of branches have sharp curves at the points where crossvein join them. A_1 is divided near the base and has two branches; the apex of the distal branch can approach CuP. A_2 has two or more branches. Crossveins are simple and H-shaped; in the interradial space, they are long, S-shaped, simple, and Y-shaped. Some crossveins are pigmented. Some RS, MA, and distal branch of CuA_1 are located in concave areas of the membrane (designated by dashed lines in Fig. 73b).

Measurements, mm. Forewing length, 13–15.

Comparison. In the forewing shape and short SC, the new species is most similar to *S. angustata* Martynov, 1937 from the Shurab II locality (Lower Jurassic of Kyrgyzstan). *S. permiana* differs from it in the narrower costal space, the greater number of anterior branches of R, and branches of RS not forming a regular anterior comb. In *S. angustata,* the costal space at the base of RS is thrice as wide as the subcostal space; R has two anterior branches; and RS forms a regular anterior comb of branches (Rasnitsyn, 1982).

Material. In addition to the holotype, paratypes PIN, nos. 3840/548, 549, 1237, 1240, 1242, 3100, and 3102-3104 from the same locality.

Genus *Sukhonia* Aristov, gen. nov.

Etymology. From the Sukhona River. Gender feminine.

Type species. *S. coriacea* sp. nov.

Diagnosis. In forewing, costal space at base of RS slightly wider than subcostal space; SC ending proximal to middle of wing. RS beginning in basal quarter of wing. Basal branch of MA fused with MP. Distal branch of CuA_1 reaching distal quarter of wing; CuA_2 with short bifurcation. Branches of RS, M, and CuA becoming noticeably thinner towards posterior wing margin. Wing membrane coriaceous, with small tubercles.

Species composition. Type species.

Comparison. The new genus differs from other geinitziids in the anastomosis of MA and MP and in the presence of bifurcation of CuA_2. In the other Geinitziidae, MA and MP are not fused, and CuA_2 is simple (Storozhenko, 1998; Aristov et al., 2009b).

Sukhonia coriacea Aristov, sp. nov.

Etymology. From the Latin *coriacea* (leather-like).

Holotype. PIN, no. 3840/796, forewing impression; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 73g, 74h). Medium-sized insect. The anterior forewing margin is weakly convex; SC has simple anterior branches. RS starts branching proximal to the middle and has three branches reaching the anterior margin and apex of the wing. M_5 is well pronounced; M is divided into MA and MP at a small distance distal to the base of RS. MA has two free branches; the anastomosis MA+MP is simple. CuA_1 has three branches; crossveins are simple and H-shaped.

Measurements, mm. Forewing length, 14.

Material. Holotype.

Family Limopteridae Sellards, 1909

Genus *Sylvaella* Martynov, 1940

Sylvaella semicolorata Aristov, sp. nov.

Etymology. From the Latin *semicolorata* (semicolored).

Holotype. PIN, no. 3840/1246, direct impression of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 74a, 75i). Medium-sized insect. The anterior forewing margin is weakly convex. The costal space near the base of RS is equal in width to the subcostal space. RS begins at the distal bound-

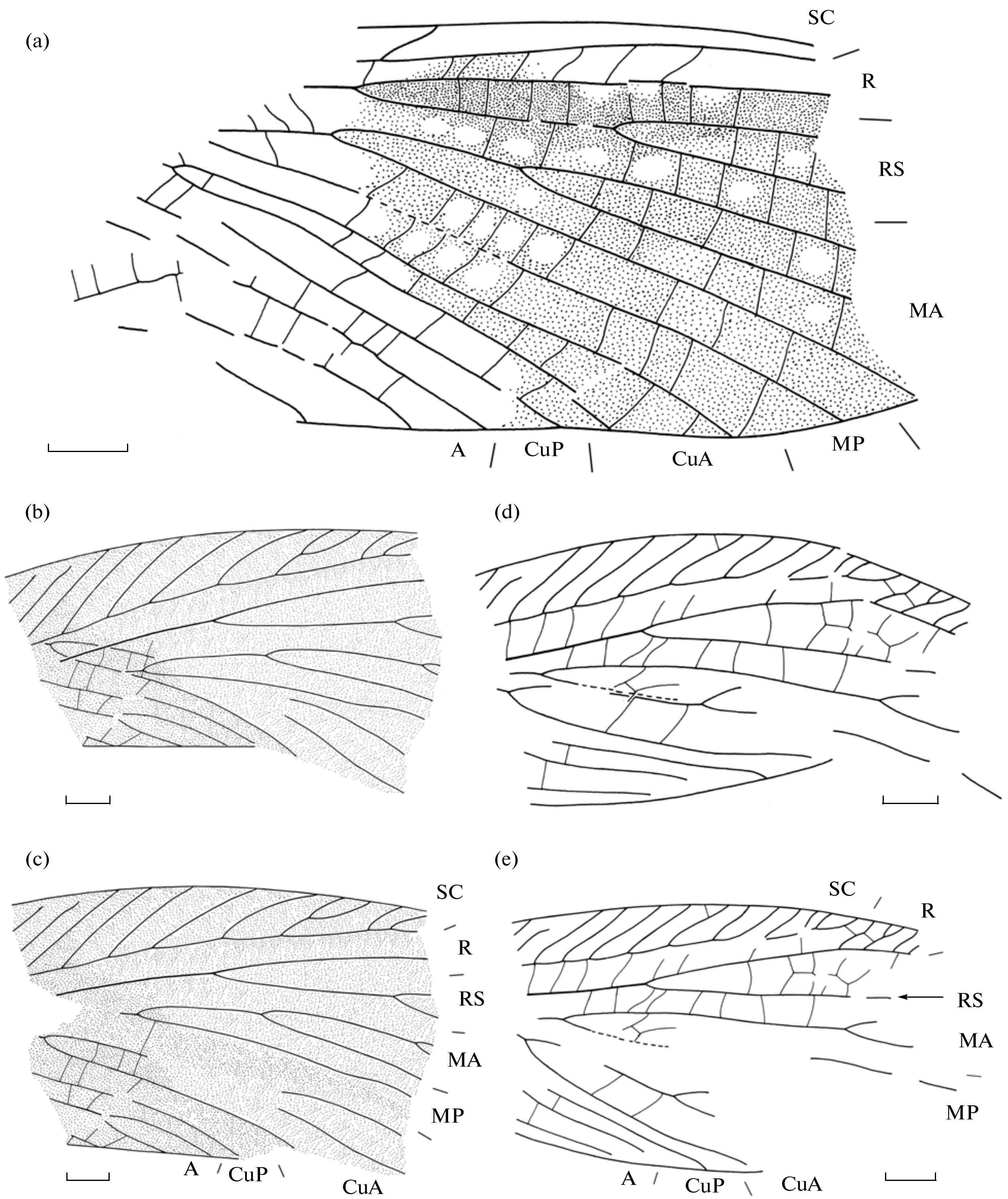


Fig. 74. Members of the family Liomopteridae from the Isady locality, Vologda Region; Severodvinian Stage, forewings: (a) *Sylvaella semicolorata* sp. nov., holotype PIN, no. 3840/1246; (b, c) *Liomofrater circumcisus* sp. nov., holotype PIN, no. 3840/1347: (b) line drawing of impression; (c) reconstruction; (d, e) *Falseshurabia transitoria* sp. nov., holotype PIN, no. 3840/1347: (d) line drawing of impression; (e) reconstruction. Scale bars, 1 mm.

ary of the basal one-third of the wing and has two or more branches. The stem MA proximal to its division into branches is parallel to R; MA has three branches; MP is simple. CuA_1 is simple; the branches of CuA are densely spaced; a very narrow space between CuA_1 and CuA_2 is dilated towards the posterior wing margin. A_1

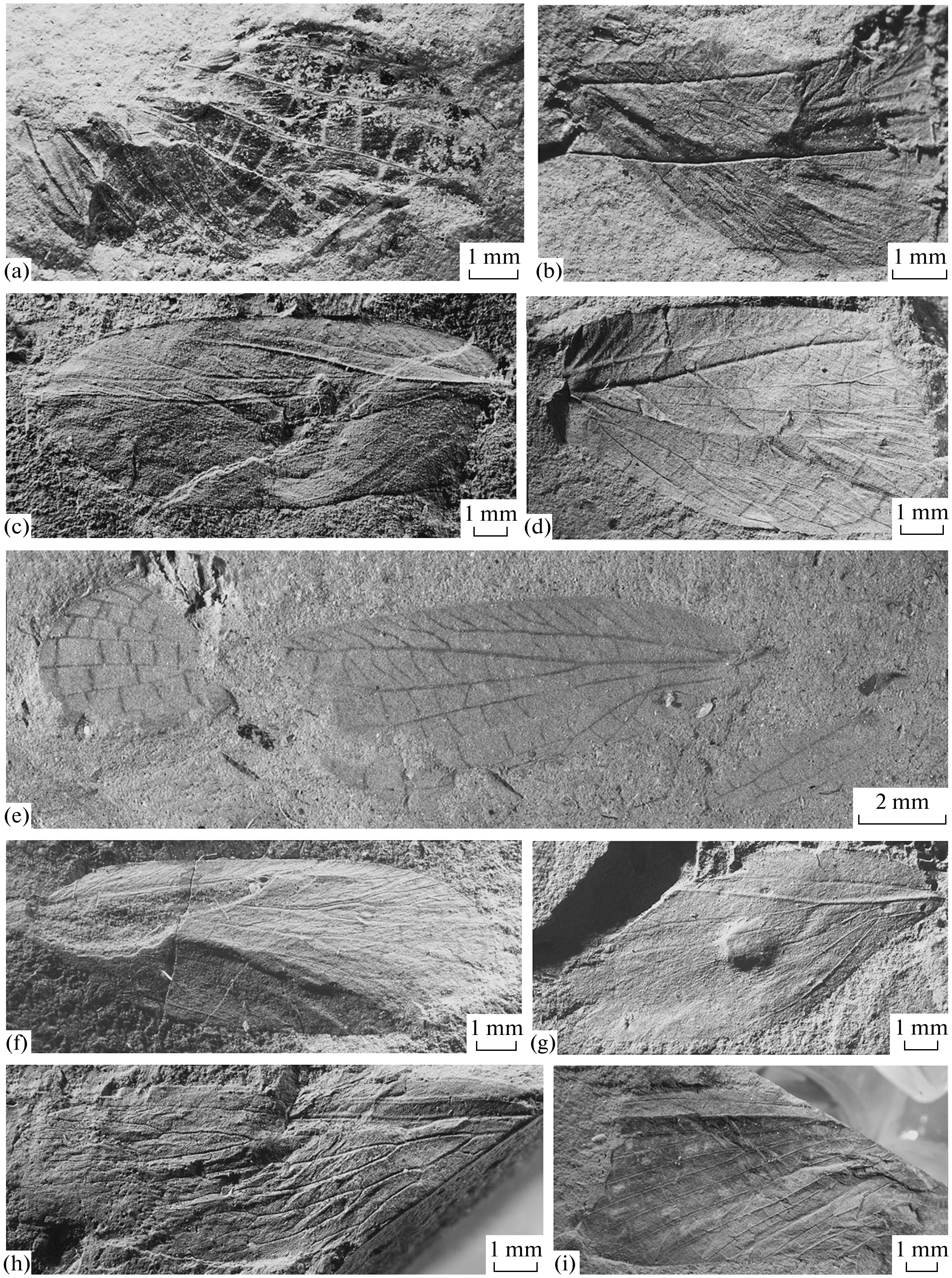


Fig. 75. Members of the families Chaulioditidae, Geinitziidae, and Liomopteridae from the Isady locality, of Vologda Region; Severodvinian Stage, forewings: (a) *Permyak involucris* sp. nov., holotype PIN, no. 3840/2091; (b) *Geinitzia subita* sp. nov., holotype PIN, no. 3840/1239; (c–g) *Shurabia permiana* sp. nov.: (c) holotype PIN, no. 3840/3101; (d) paratype PIN, no. 3840/1242; (e) paratype PIN, no. 3840/549 (three fragments of one wing preserved close to each other); (f) paratype PIN, no. 3840/1237; (g) paratype PIN, no. 3840/548; (h) *Sukhonia coriacea* sp. nov., holotype PIN, no. 3840/796; (i) *Sylvaella semicolorata* sp. nov., holotype PIN, no. 3840/1246.

is simple; A_2 has two or more branches. Crossveins are simple, straight, slightly S-shaped in the subcostal and radial spaces. The entire membrane, except for the preradial space, is evenly pigmented.

Measurements, mm. Forewing length, about 14.

Comparison. The new species is most similar to *S. ovalis* Aristov, 2010 from the Lower Permian Tyul'kino locality, Perm Region and differs from it in the narrower costal space and in the strongly narrowed space between the branches of CuA. In *S. ovalis,* the costal space at the base of RS is 1.5 as wide as the subcostal space; the space between the branches of CuA is not narrowed (Aristov, 2010).

Material. Holotype.

Genus *Liomofrater* Aristov, gen. nov.

Etymology. From the generic name *Lioma* Kukalová, 1964 and the Latin *frater* (brother). Gender masculine

Type species. *L. circumcisus* sp. nov.

Diagnosis. Costal space in basal one-third of forewing occupying more than one-third of its width. SC with long anterior branches strongly inclined and curved towards anterior margin of wing. RS beginning close to middle of wing. M divided into MA and MP at distal boundary of basal one-third of wing. Apex of CuA_2 straight. A_1 with two branches.

Species composition. Type species.

Comparison. The new species is most similar to *Falseshurabia* gen. nov. in the width of the precostal space (a unique character of liomopterids) and differs from it in the anterior branches of SC strongly inclined and curved towards the anterior wing margin, the RS beginning near the middle of the wing, and the straight apex of CuA_2. In *Falseshurabia,* the anterior branches of SC are moderately long, S-shaped; RS begins in the basal one-third of the wing; and the apex of CuA_2 is S-shaped (see below).

Liomofrater circumcisus Aristov, sp. nov.

Etymology. The Latin *circumcisus* (abridged).

Holotype. PIN, no. 3840/1347, direct impression of incomplete distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 74b, 74c, 77a). Medium-sized insect. The anterior wing margin is weakly convex. The costal space near the base of RS is twice as wide as the subcostal space. SC has simple and Y-shaped anterior branches, reaches the wing apex. RS has two or more branches. MA is divided distal to the base of RS and has three or more branches; MP is simple. CuA_1 is divided close to the middle of its extent and has two branches. Crossveins are simple.

Measurements, mm. Forewing length, about 15.

Material. Holotype.

Genus *Falseshurabia* Aristov, gen. nov.

Etymology. From the Latin *falsus* (false) and the generic name *Shurabia.* Gender feminine.

Type species. *F. transitoria* sp. nov.

Diagnosis. Costal space in basal one-third of forewing occupying more than half of its width. Costal space at base of RS somewhat wider than subcostal space. Anterior branches of SC moderately long, S-shaped. RS beginning in basal one-third of wing. M divided into MA and MP in basal quarter of wing. Apex of CuA_2 S-shaped. A_1 simple.

Species composition. Type species.

Comparison. The new genus is most similar to *Liomofrater* gen. nov., in the width of the precostal space (a unique character of liomopterids) and differs from it in the moderately long S-shaped anterior branches of SC, the RS beginning in the basal one-third of the wing, and the S-shaped apex of CuA_2. In *Liomofrater,* the anterior branches of SC are strongly inclined and curved towards the anterior wing margin, RS begins near the middle of the wing, and the apex of CuA_2 is straight (see above).

Falseshurabia transitoria Aristov, sp. nov.

Etymology. From the Latin *transitoria* (transitional).

Holotype. PIN, no. 3840/1240, direct impression of incomplete distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 74d, 74e, 77b). Medium-sized insect. The anterior wing margin is weakly convex. SC ends in the distal one-third of the wing. The costal space near the base of RS is twice as wide as the subcostal space. SC has simple anterior branches; the anterior branches of R are simple and Y-shaped. RS is simple or has two branches. MA, MP, and CuA_1 have two branches each; CuA_1 is divided close to the middle of its extent. Crossveins are simple, H-shaped, and forming a double row of cells. A_2 has two or more branches.

Measurements, mm. Forewing length, about 14.

Material. Holotype.

Family Mesorthopteridae Tillyard, 1916

Genus *Mesoidelia* Storozhenko, 1996

Mesoidelia gorochovi Aristov, sp. nov.

Etymology. In honor of the entomologist A.V. Gorochov.

Holotype. PIN, no. 3840/652, direct impression of forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 76a, 77c). Medium-sized insect. The anterior wing margin is weakly convex. The costal space is wide, twice as wide as the subcostal

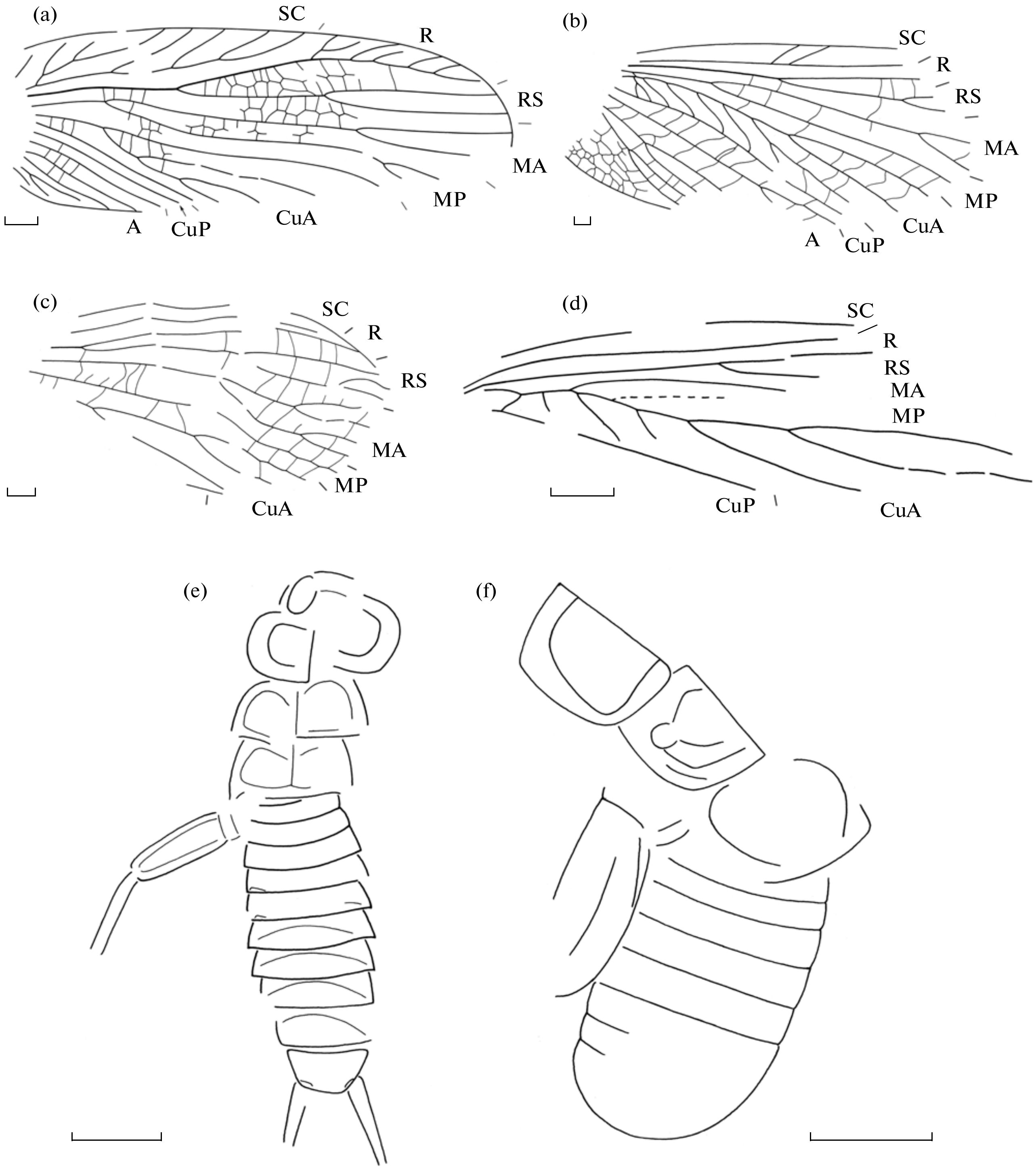


Fig. 76. Members of the families Mesorthopteridae, Megakhosaridae, Blattogryllidae, and Grylloblattidae incertae sedis from the Isady locality, Vologda Region; Severodvinian Stage: (a) *Mesoidelia gorochovi* sp. nov., holotype PIN, no. 3840/652, forewing; (b) *Parakhosara reticulata* sp. nov., holotype PIN, no. 3840/1248, forewing; (c) *Abbrevikhosara ovoidea* sp. nov., holotype PIN, no. 3840/1249, forewing; (d) *Baharellinus porrectus* sp. nov., holotype PIN, no. 3840/1244, forewing; (e) *Issadonympha oculea* sp. nov., holotype PIN, no. 3840/553, nymph, habitus; (f) *Kenguronympha lenta* sp. nov., holotype PIN, no. 3840/1647, nymph, habitus. Scale bars, 1 mm.

space at the level of the base of RS. SC ends proximal to the distal one-third of the wing; the anterior branches of SC are simple, relatively short and long, branching, strongly inclined; distal to the base of RS, R curves towards the anterior wing margin; the anterior branches of R are short, simple, and dichotomous.

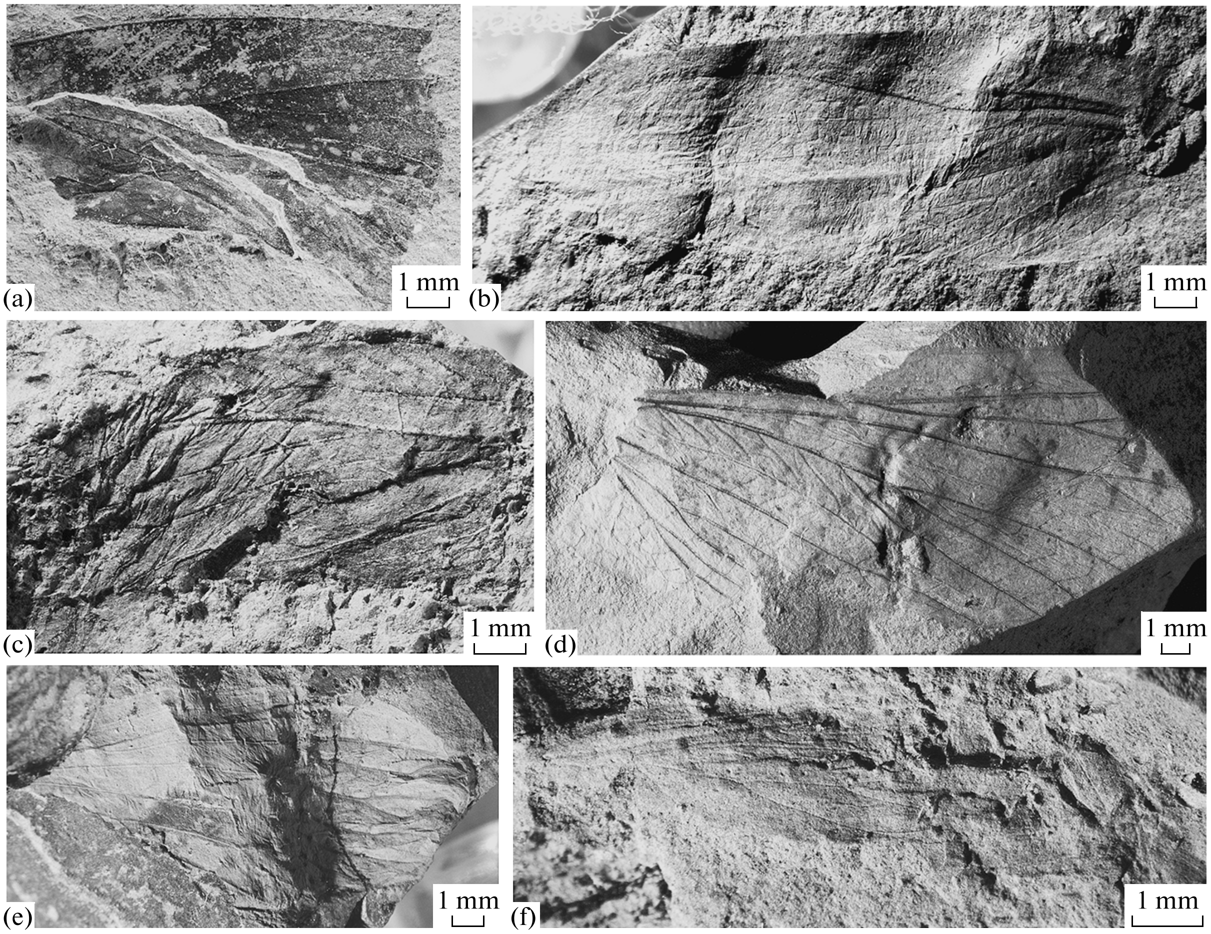


Fig. 77. Members of the families Liomopteridae, Mesorthopteridae, Megakhosaridae, and Blattogryllidae from the Isady locality, Vologda Region; Severodvinian Stage, forewings: (a) *Liomofrater circumcisus* sp. nov., holotype PIN, no. 3840/1347: (b) *Falseshurabia transitoria* sp. nov., holotype PIN, no. 3840/1347; (c) *Mesoidelia gorochovi* sp. nov., holotype PIN, no. 3840/652; (d) *Parakhosara reticulata* sp. nov., holotype PIN, no. 3840/1248; (e) *Abbrevikhosara ovoidea* sp. nov., holotype PIN, no. 3840/1249; (f) *Baharellinus porrectus* sp. nov., holotype PIN, no. 3840/1244.

RS begins at the distal boundary of the basal one-third of the wing, is divided in the distal one-third of the wing, and has two branches. The base of M is parallel to R, divided into MA and MP at the level of the first bifurcation of CuA. MA and MP have short simple bifurcations. CuA starts branching in the basal quarter; it is pectinate anteriorly and has four branches, which reach the distal quarter of the wing. The distal part of the intercubital space is narrow. A_1 is simple; A_2 has five branches. Crossveins are simple and form two or three rows of cells.

Measurements, mm. Forewing length, 16.

Comparison. The new species is most similar to *M. faceta* Storozhenko, 1996 from the Middle to Upper Triassic of Kyrgyzstan, differing from it in the anteriorly pectinate CuA. In *M. faceta,* CuA branches irregularly (Storozhenko, 1996).

Material. Holotype.

Family Megakhosaridae Sharov, 1961

Genus *Parakhosara* Storozhenko, 1993

Parakhosara reticulata Aristov, sp. nov.

Etymology. From the Latin *reticulata* (netlike).

Holotype. PIN, no. 3840/1248, direct impression of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 76b, 77d). Large insect. The anterior forewing margin is straight. The costal space at the level of the base of RS is somewhat wider than the subcostal space. The anterior branches of SC are simple, more or less strongly inclined. RS begins in the basal quarter of the wing and starts branching near the middle of the wing; the interradial space is narrow. In the basal half of the wing, MA has two branches, and MP is simple, without a trace of desclerotization. CuA has three branches; it starts branching near the middle, proximal to the base of RS and lacks a curvature at the point of division. The posterior branches of CuA are widely spaced, simple and Y-shaped; the last of these branches diverges from the basal branch of CuA. A_1 has two branches; A_2 is dichotomous and has four branches. A large part of the wing between CuA_2 and the posterior wing margin is occupied by a network of irregular cells. Crossveins are simple and Y-shaped, straight, and S-shaped.

Measurements, mm. Forewing length, about 50.

Comparison. The new species is most similar to *P. kopylovi* Aristov, 2009 from Isady, from which it differs in the larger size and wider costal space. In *P. kopylovi*, the forewing is about 15 mm long and the costal space near the base of RS is equal in width to the subcostal space (Aristov, 2009c).

Remarks. The situation in which about one-third of the anal space is occupied by a network of irregular cells is unique among megakhosarids. However, the loss of the anal area in many megakhosarid specimens prevents the establishment of a new genus based on this character.

Material. Holotype.

Genus *Abbrevikhosara* Aristov, gen. nov.

Etymology. From the Latin *abbrevio* (shorten) and the generic name *Khosara* Martynov, 1937. Gender feminine.

Type species. *A. ovoidea* sp. nov.

Diagnosis. Forewing twice as long as wide. Costal space at base of RS equal in width of subcostal space. RS beginning in basal quarter of wing; interradial space narrow in basal half of wing. Intermedial space dilated. CuA straight, branching in basal one-third, its anterior branch reaching distal quarter of wing.

Species composition. Type species.

Comparison. *Abbrevikhosara* differs from other genera of the family in the broad wing and the CuA reaching the distal quarter of the wing. In other megakhosarids, the wing is three to four times as long as wide, with the exception of the clearly distorted wings from the Middle–Upper Triassic Madygen locality in Kyrgyzstan. In Isady, changes in the wing proportions caused by deformations in enclosing matter have not been recorded. In other Megakhosaridae, CuA ends proximal to the distal quarter of the wing (Storozhenko, 1998; Aristov, 2008b; 2009a).

Remarks. Although posterior branches of CuA, which show distinctive features of Megakhosaridae, are not preserved in the impression, the genus is assigned to this family based on the narrow costal space, the RS beginning proximally and forming a narrow interradial space, and the distally branching CuA. The wing proportions of *A. ovoidea* are atypical of megakhosarids. The wing in question is probably brachypterous.

Abbrevikhosara ovoidea Aristov, sp. nov.

Etymology. From the Latin *ovoidea* (egg-shaped).

Holotype. PIN, no. 3840/1249, direct impression of incomplete distorted forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 76c, 77e). Medium-sized insect. The anterior forewing margin is convex. RS starts branching distal to the middle of the wing and has three branches. MA is dichotomous and has four branches; it starts branching distal to the middle of the wing; MP is simple. CuA has three branches; MP and distal branches of CuA have sharp curves at points where crossveins join them. Crossveins are simple, straight and curved.

Measurements, mm. Forewing length, about 15; maximum width, 7.3.

Material. Holotype.

Family Blattogryllidae Rasnitsyn, 1976

Genus *Baharellinus* Storozhenko, 1992

Baharellinus porrectus Aristov, sp. nov.

Etymology. The Latin *porrectus* (extended).

Holotype. PIN, no. 3840/1244, direct impression of incomplete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 76d, 77f). Medium-sized insect with narrow wings. The anterior forewing margin is weakly convex. The costal space at the base of the wing is slightly narrower than the subcostal space. RS begins in the basal one-third of the wing and does not form an anastomosis with MA. M has a free base; it is fused with CuA over a large part of its extent. MA and MP diverge from CuA in separate stems and do not branch proximal to the middle of the wing. CuA branches distal to its middle, forming three branches, the distal one enters the distal quarter of the wing. Three preserved posterior branches of CuA are long, S-shaped, widely spaced.

Measurements, mm. Forewing length, about 21.

Comparison. The new species is most similar to *B. dimidiatus* Storozhenko, 1992 from the Middle–Upper Triassic Madygen locality in Kyrgyzstan and differs from it in the presence of a free base of M and in the distal branch of CuA reaching the distal quarter of the wing. In *B. dimidiatus,* the base of M is completely fused with CuA, the distal branch of which ends proximal to the distal one-third of the wing (Storozhenko, 1992).

Material. Holotype.

Grylloblattida incertae sedis

Genus *Issadonympha* Aristov, gen. nov.

Etymology. From the Isady locality and the Greek *nymphe* (nymph). Gender feminine.

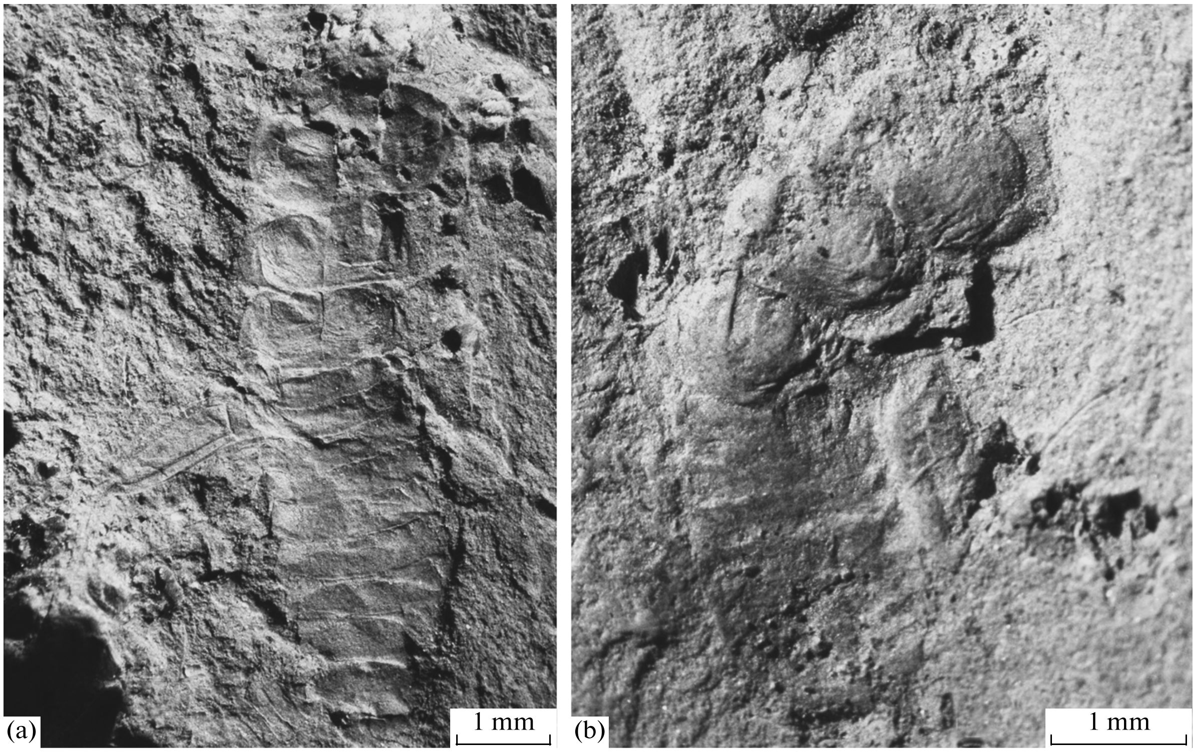


Fig. 78. Grylloblattidae incertae sedis from the Isady locality, Vologda Region; Severodvinian Stage, nymphs, habitus: (a) *Issadonympha oculea* sp. nov., holotype PIN, no. 3840/553; (b) *Kenguronympha lenta* sp. nov., holotype PIN, no. 3840/1647.

Type species. *I. oculea* sp. nov.

Diagnosis. Head large, transverse, with large eyes. Pronotum transverse, smaller than head, with wide ring of paranota. Mesonotum and metanotum trapezoid, posteriorly dilated, comparable in size with pronotum. Hindlegs of medium length. Abdomen fusiform, longer than head and thorax; cerci short, one-segmented.

Species composition. Type species.

Comparison. The new genus is most similar to *Kaltanympha* Sharov, 1961 from the Kazanian deposits of Kemerovo Region and Severodvinian deposits of Evenkia; the new genus differs from it in the wider paranota and in the one-segmented cerci. In *Kaltanympha,* the paranota are narrower, and the cerci have more than one segment (Aristov et al., 2006).

Issadonympha oculea Aristov, sp. nov.

Etymology. From the Latin *oculea* (sharp-sighted).

Holotype. PIN, no. 3840/553, part and counterpart of nymph; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 76e, 78a). The pronotum is rounded trapezoid, with convex margins. The lateral margins of the circular paranota are wider than the anterior and posterior margins. The femora have longitudinal ridges and are twice as wide as the tibiae. The abdominal segments become longer towards the apex; the apical tergite is the longest, trapezoid, slightly asymmetrical.

Measurements, mm. Body length, 5.8.

Material. Holotype.

Genus *Kenguronympha* Aristov, gen. nov.

Etymology. From the Russian *kenguru* (kangaroo) and the Greek *nymphe* (nymph). Gender feminine.

Type species. *K. lenta* sp. nov.

Diagnosis. Pronotum with narrow ring of paranota, dilated posteriad, somewhat wider than long. Mesonotum transverse, equal in size to pronotum; metanotum approximately as long as wide; metanotum smaller than pronotum and mesonotum. Metafemur strong, longer than pronotum, approximately thrice longer than wide. Abdomen short, thick, shorter than thorax.

Species composition. Type species.

Comparison. The new genus is most similar to *Issadonympha* from Isady and differs from it in the longer thoracic segments, strong metafemur, and short, thick abdomen. In *Issadonympha,* the thoracic segments are more transverse, metafemora are narrower, and the abdomen is longer and narrower (see above).

Kenguronympha lenta **Aristov, sp. nov.**

Etymology. From the Latin *lenta* (slow).

Holotype. PIN, no. 3840/1647, part and counterpart of nymph; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 76f, 78b). The pronotum is trapezoid, with more or less straight margins. The lateral margins of circular paranota dilate anteriad. The femora have longitudinal ridges and are twice as wide as the tibiae. Abdominal segments VI and V are the widest.

Measurements, mm. Body length, about 6.

Material. Holotype.

2.7. A New Stonefly Assemblage (Insecta: Perlida = Plecoptera) from the Upper Permian Deposits of Northern European Russia

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The Upper Permian Isady locality (Severodvinian Stage of the Vologda Region) has yielded the richest known stonefly assemblage. New stonefly genera and species of the suborder Perlina are described here: *Boreoperlidium borealis* gen. et sp. nov. (Eustheniidae), *Properla issadensis* sp. nov., *Kargaloperla decipiens* sp. nov., *K. furcata* sp. nov. (Palaeoperlidae), all from wings, and the nymph *Issadoperla permiana* gen. et sp. nov. (Tshekardoperlidae). The family of the new genus and species *Mirumoperla multinerva* gen. et sp. nov. described from an isolated wing fragment, remains undetermined. All new species of the suborder Nemourina belong to the family Palaeonemouridae and are described from isolated wings. The new genus and species *Votaknemoura admiranda* gen. et sp. nov. and the new species *Palaeonemoura antrorsa* sp. nov., *P. amica* sp. nov., *Palaeotaeniopteryx dejecta* sp. nov., *P. constricta* sp. nov., *P. adjecta* sp. nov., *P. succida* sp. nov., *P. amissa* sp. nov., *P. mira* sp. nov., *P. fixa* sp. nov., *Palaeonemourisca diluta* sp. nov., and *P. formalis* sp. nov. are also described from Isady. Two new species, *Palaeonemoura repleta* sp. nov. and *Palaeonemourisca strigosa* sp. nov., are described from the Chepanikha locality. Identification keys to species of the family Palaeonemouridae are provided.

The purpose of this study is to describe new stonefly taxa from the Upper Permian deposits of the Chepanikha (Urzhumian Stage of Udmurtia) and Isady (Severodvinian Stage of Vologda Region) localities. Two new species are described from Chepanikha; others are from Isady. For a detailed discussion of these localities, see Chapter 1.

In the Chepanikha locality, 13 stonefly specimens have been collected in deposits of the Urzhumian Stage of the Middle Permian. The two new species *Palaeonemoura repleta* sp. nov. and *Palaeonemourisca strigosa* sp. nov. are described from isolated whole forewings found in these deposits. Other specimens are so fragmentary that they remain undetermined; they probably belong to the family Palaeonemouridae.

In Isady, stoneflies are represented almost exclusively by isolated wings, usually in the form of incomplete fragments (58 specimens) and by many fossil nymphs preserved very poorly and fragmentarily (about 200 specimens). Most stonefly taxa from this locality are described from forewings; only two new species are described from a complete very well-preserved hind wing, and only one nymph is described as a new species. Three stonefly species of the family Palaeonemouridae Sinitshenkova, 1987 have already been described from Isady (*Palaeonemoura issadensis* Sinitshenkova et Aristov, 2010, *Palaeotaeniopteryx laeta* Sinitshenkova et Aristov 2010, and *P. triternata* Sinitshenkova et Aristov 2010), and one specimen was identified to the genus *Kargaloperla* Sinitshenkova, 1987 of the family Palaeoperlidae Sharov, 1961 (Sinitshenkova and Aristov, 2010).

Among new materials collected in Isady, stoneflies of both suborders, Perlina and Nemourina, have been found. Among Perlina, two families characteristic of the Permian, Eustheniidae Tillyard, 1921 (Gripopterygomorpha) and Palaeoperlidae Sharov, 1961 (Perlomorpha), can be identified from wings. In the family Palaeoperlidae, the new species *Properla issadensis* sp. nov. and two new species of the genus *Kargaloperla* Sinitshenkova, 1987 are described. Members of the genus *Properla* Sharov, 1961 are very infrequent; the type species is known from a single whole fossil wing from the Upper Permian of Siberia (Sinitshenkova, 1987). Although the fossil wing described below is only a rather small fragment, it deserves description, because it displays important diagnostic characters of the genus, such as the clearly convex anterior wing margin, wide radial space in the apical part of the wing, numerous crossveins in the costal space, and rather small size. The family which includes the new Perlomorpha genus and species *Mirumoperla multinerva* sp. nov. remains uncertain.

Species of the family Eustheniidae occur in the modern fauna only in the Southern Hemisphere. The only known extinct member of this family, *Stenoperlidium permianum* Tillyard, 1935, was described from the Upper Permian of Australia (Tillyard, 1935). Two fossil forewings from Isady described below as *Boreoperlidium borealis* sp. nov., represent the first Eustheniidae in the Northern Hemisphere, giving evidence of the global distribution of this family in the remote past. For comparison with the new genus, it is expedient to redescribe the genus *Stenoperlidium* Tillyard, 1935, which is performed based only on the photograph provided by Tillyard (1935). Unfortunately, it is impossible for me to reexamine the type specimen of *S. permianum* Tillyard, 1935 in the near future.

Another specimen of Gripopterygomorpha from Isady is assigned to the family Euxenoperlidae Enderlein, 1909, which has previously been known exclusively from the Southern Hemisphere. This fragment of a crumpled wing (specimen PIN, no. 3840/603) is identified provisionally as a member of the genus *Gondwanoperlidium* Pinto et Purper, 1978. Although this specimen is poorly preserved and impossible to identify more precisely, it should be mentioned, because wings of Perlina occur in the fossil record considerably less frequently than those of Nemourina. The families Eustheniidae and Euxenoperlidae, which have previously been considered to be Gondwanan, probably had a much wider distribution in the Permian.

One fossil nymph is described below in the family Tshekardoperlidae Sinitshenkova, 1987 as a new genus and species, *Issadoperla permiana* gen. et sp. nov. To date, members of this family have only been known from the Early Permian of the Perm Region. Two genera have been described from nymphs found in the well-known Chekarda locality: *Tshekardoperla* Sinitshenkova, 1987, including three species, and the monotypic genus *Sylvoperlodes* Sinitshenkova, 1987 (Sinitshenkova, 1987).

Members of Nemourina are considerably more abundant and diverse, but they all belong to one family, Palaeonemouridae Sharov, 1961, and four genera, three of which were described earlier, *Palaeonemoura* Sharov, 1961, *Palaeotaeniopteryx* Sharov, 1961, and *Palaeonemourisca* Sinitshenkova, 2004, and one, *Votaknemoura* gen. nov., is new. Both previously described species, *P. issadensis* Sinitshenkova et Aristov, 2010 (specimen PIN, no. 3840/630) and *P. laeta* Sinitshenkova et Aristov, 2010 (specimen PIN, no. 3840/489 and 631), are recorded in the newly collected material. In addition, two new species are described in the genus *Palaeonemoura, P. antrorsa* sp. nov. and *P. amica* sp. nov.; and seven new species are described in the genus *Palaeotaeniopteryx*: *P. dejecta* sp. nov., *P. constricta* sp. nov., *P. adjecta* sp. nov., P. succida sp. nov., *P. amissa* sp. nov., *P. fixa* sp. nov., and *P. mira* sp. nov. The last two species are described from well preserved whole isolated hindwings. Whole hindwings with distinct venation occur considerably less frequently than forewings; therefore, it is expedient to describe new species from hindwings. The morphology of both forewings and hindwings is only known in one species, *P. elegans* Sharov, 1961 from the Upper Permian of the Kuznetsk Basin. It appears impossible to associate new species with forewings from Isady. Two new species are described in the genus *Palaeonemourisca, P. diluta* sp. nov. and *P. formalis* sp. nov.

The ratio of the number of *Palaeonemoura* and *Palaeotaeniopteryx* differs in different localities. It is correct to compare Late Permian localities of Isady and Novo-Aleksandrovka (Orenburg Region), wherefrom a great number of species of these genera have been described (Sinitshenkova, 2004). A total of three *Palaeonemoura* species and seven *Palaeotaeniopteryx* species are known from Isady, whereas six *Palaeonemoura* and only two *Palaeotaeniopteryx* are known from Novo-Aleksandrovka.

Most stonefly specimens from Isady remain undescribed, because they are fragmentary and poorly preserved, but nine of them are assigned to the genus *Palaeotaeniopteryx,* judging from the presence of a long RS pedicel.

The fossil stonefly assemblage found in Isady, represented by 22 species, is the richest and the most taxonomically diverse assemblage of fossil stoneflies known from a single locality. This is probably accounted for by the fact that stonefly remains were transported to the burial by streams from an extensive basin. The preservation type of stoneflies in the oryctocoenosis, with only isolated wings of adults and, even more often, their fragments, suggests that they were long transported to the burial. This assumption is confirmed by abundant fossil nymphs and exuviae, damaged and mixed, so that they cannot be identified. The stoneflies probably lived in the streams flowing into the lake, rather than in the lake where sediments were accumulated. This picture complies well with the landscape reconstruction provided for the Isady locality (see Chapter 1.2.2).

The rich stonefly assemblage found in Isady suggests for the first time that this insect group played in Permian river biocoenoses a much more important role than in the later periods of this order's history. In the Permian fresh waterbodies, dragonfly nymphs, important benthic predators, were still absent; mayflies were apparently infrequent and megalopteran finds are scarce. Schizophoroid beetles, which could also have an aquatic mode of life, appeared for the first time in the Late Permian. Caddisfly larvae probably also led an aquatic mode of life, but they have not been found in Permian deposits. The scanty set of freshwater insects suggests that the role of predators could have been played by stoneflies of the suborder Perlina, while members of the suborder Nemourina, represented by several size classes, were responsible for breaking organic remains and detritophagy (Sinitshenkova, 2011). Stoneflies lived also in rapids, as evidenced by the unique find of the rheophilic stonefly *Barathronympha victima* Sinitshenkova, 1987 in Lower Permian deposits of the Perm Region (Sinitshenkova, 1987).

I am deeply grateful to D.S. Aristov for drawing the wing of *Stenoperlidium permianum.*

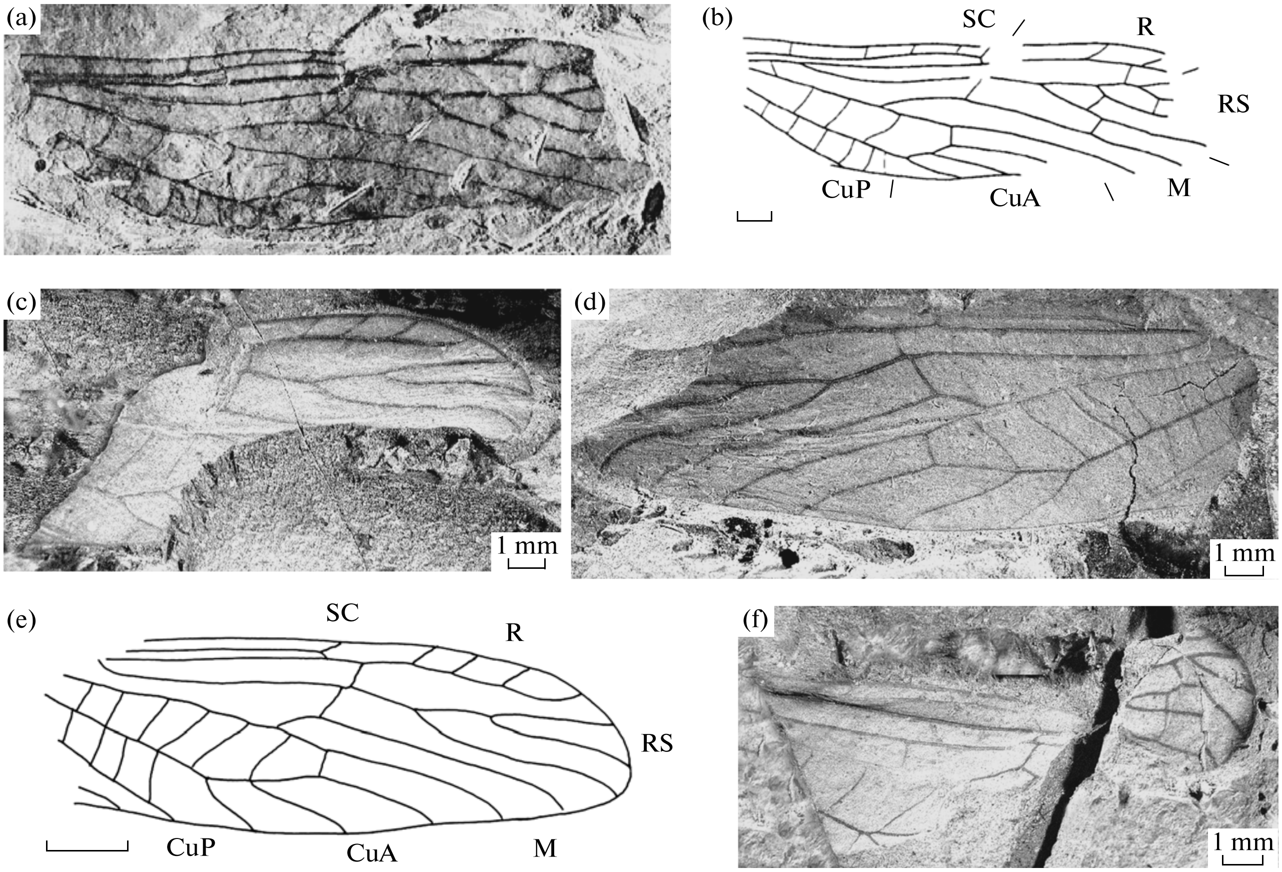

Fig. 79. Stoneflies of the suborder Perlina, infraorder Gripopterygomorpha: (a, b) *Stenoperlidium permianum*; Upper Permian of Australia; (c–f) Isady locality, Vologda Region; Severodvinian Stage: (c–e) *Boreoperlidium borealis* gen. et sp. nov., holotype PIN, no. 3840/604, wing fragment; (f) *?Gondwanoperlidium*, specimen PIN, no. 3840/603. Scale bars in (b, e), 2 mm.

Order Perlida (=Plecoptera) Latreille, 1802

Suborder Perlina Latreille, 1802

Infraorder Gripopterygomorpha Enderlein, 1909

Family Eustheniidae Tillyard, 1921

Genus *Stenoperlidium* Tillyard, 1935

Type species. *S. permianum* Tillyard, 1935; Upper Permian of Australia.

Diagnosis. Adult. In forewing, RS with four branches, M branching considerably proximal to bifurcations of CuA. CuA reaching wing margin in three branches, two anterior ones pectinately diverging from main stem and almost equal in width. Straight infrequent crossveins formed between branches of RS, between R and anterior branch of RS, and between posterior branch of RS and MA.

Species composition. Type species.

Stenoperlidium permianum Tillyard, 1935

Description (Figs. 79a, 79b). Adult. In the forewing, SC joins R almost at the level of r–rs; rs–m diverges from RS almost at the level of r–rs and joins MA markedly distal to its base. Four crossveins are present in the preserved part of the costal space; two crossveins are visible in the preserved part of the pterostigmal area. Three crossveins are present in the medial space; six crossveins are present in the cubital space.

Measurements, mm. Length of forewing fragment, 22.5; total forewing length, about 25.

Remarks. In the monograph by Sinitshenkova (1987, p. 21, text-fig. 14), the figure of *Gondwanoperlidium triassicum* (Riek, 1956) is mistakenly captioned as *Stenoperlidium permianum*. The description of the genus *Stenoperlidium* and the species *S. permianum* as well as Fig. 79a provided here are based on the photograph by Tillyard (1935).

Boreoperlidium Sinitshenkova, gen. nov.

Etymology. From the Latin *borealis* (northern) and the generic name *Perlidium*.

Type species. *B. borealis* sp. nov. Upper Permian of Vologda Region.

Diagnosis. Adult. In forewing, RS with three branches, M branching somewhat distal to first division of CuA, CuA reaching wing margin in three branches, its anterior fork wider than posterior one. Between RS branches, between R and anterior branch of RS, and between posterior branch of RS and MA crossveins absent.

Species composition. Type species.

Comparison. The new genus is clearly distinguished from the genus *Stenoperlidium,* which has a similar venation, by the smaller number of RS branches, more distal branching of M, wider anterior fork of CuA, and the absence of crossveins between RS branches, between R and anterior branch of RS, and between posterior branch of RS and MA.

Boreoperlidium borealis **Sinitshenkova, sp. nov.**

Etymology. The Latin *borealis* (northern).

Holotype. PIN, no. 3840/604, part and counterpart of incomplete forewing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 79c–79e). Adult. In the forewing, SC joins R proximal to r–rs; c-sc is long and reaches the wing margin markedly distal to the apex of SC; rs–m diverges from RS at the level of, or slightly proximal to, r–rs and joins MA markedly distal to its base. The preserved part of the costal space has two crossveins; the pterostigmal area has three crossveins. The medial space has seven crossveins; the preserved part of the cubital space has four crossveins.

Measurements, mm. Length of forewing fragment (holotype), 17.0; total forewing length, about 20; length of forewing fragment, (paratype) 16.

Material. In addition to the holotype, paratype PIN, no. 3840/1609: crumpled fragment of a large wing, with the characteristic branching of CuA.

Family Euxenoperlidae Enderlein, 1909

Specimen PIN, no. 3840/603, a rather small, crumpled wing fragment (Fig. 79f), from he Isady locality is close to species of the genus *Gondwanoperlidium* Pinto et Purper, 1978 because of several longitudinal veins characteristically drawn together by crossveins and reaching the wing margin at the apex. The wing fragment is 14.0 mm long; complete forewing was about 20 mm long. In the genus *Gondwanoperlidium,* three species from the Triassic of Argentina and Australia have been described (Pinto and Purper, 1978).

Infraorder Perlomorpha Latreille, 1802

Family Tshekardoperlidae Sinitshenkova, 1987

Genus *Issadoperla* Sinitshenkova, gen. nov.

Etymology. From the Isady locality and the generic name *Perla* Geoffroy 1762.

Type species. *I. permiana* Sinitshenkova, sp. nov.

Diagnosis. Nymph. Medium-sized stonefly with long pronotum and short legs. Mesothorax and metathorax with rounded, widely set wing primordia. Two protarsomeres short, subequal in length.

Species composition. Type species.

Comparison. The new genus is clearly distinguished from *Tshekardoperla* Sinitshenkova, 1987 by the narrow and long pronotum and from *Sylvoperlodes* Sinitshenkova, 1987 by the shorter wing pads. Both known genera have been described from the Lower Permian of the Cis-Ural Region, from the unique Chekarda locality.

Issadoperla permiana **Sinitshenkova, sp. nov.**

Etymology. From the Permian Period.

Holotype. PIN, no. 3840/497, part and counterpart of nymph, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 80). Nymph. The head is transverse, shorter than the pronotum. The antennomeres are short. The mandibles are asymmetrical, with rather small denticles apically and a wide molar part. The pronotum is long, 1.5 times longer than wide; the mesothorax and metathorax are wider than the prothorax and have short wing pads with broadly rounded apices. The foreleg is slightly more than half as long as the body; the femur is somewhat shorter than the tibia and twice wider; the tibia is 2.5 times longer than the tarsus. The external margin of the femur and tibia has a dense fringe of long swimming hairs. The abdomen is fusiform, with the proximal and distal segments narrower than the middle segments. The caudal filaments consist of short segments.

Measurements, mm. Length of preserved part of body, 16.0; profemur length, 3.1; protibia length, 3.5; protarsus length, 1.7.

Material. Holotype.

Family Palaeoperlidae Sharov, 1961

Genus *Properla* Sharov, 1961

Properla issadensis **Sinitshenkova, sp. nov.**

Etymology. From the Isady locality.

Holotype. PIN, no. 3840/425, rather small forewing fragment without cubital and anal parts; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 81a, 81b). Adult. The dilated pterostigmal area has five clearly discernible oblique crossveins. RS has three branches; RS and its anterior branch are dichotomizing; the pedicel of the fork of the anterior branch is almost as long as the fork; the apices of the branches of RS noticeably diverge reaching the wing margin.

Measurements, mm. Length of wing fragment, 10; total forewing length, about 13.

Comparison. The new species is clearly distinguished from *P. tungussica* by the smaller number of

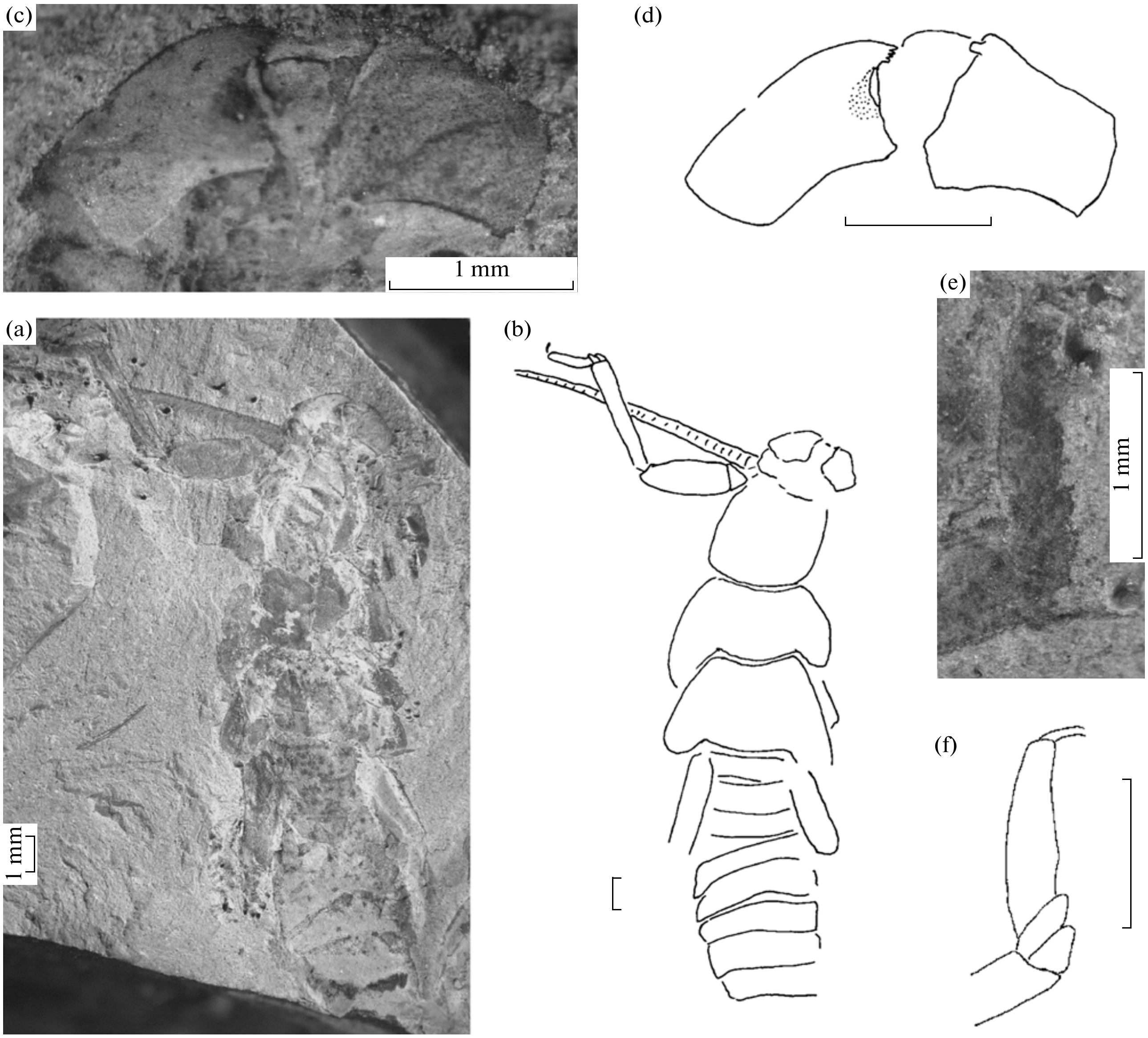

Fig. 80. Nymph of *Issadoperla permiana* gen. et sp. nov., holotype PIN, no. 3840/497; Isady locality, Vologda Region; Severodvinian Stage: (a, b) habitus; (c, d) mandibles; (e, f) metatarsus. Scale bar, 1 mm.

branches of RS, the dichotomous branching of RS and its anterior branch, and the somewhat larger size.

Material. Holotype.

Genus *Kargaloperla* Sinitshenkova, 1987

Type species. *K. exuperata* Sinitshenkova, 1987; Upper Permian, Orenburg Region.

Species composition. Four species from the Upper Permian: one from the Orenburg Region (Kargala), one from the East Kazakhstan Province (Karaungir-II), and two new species from the Vologda Region.

Kargaloperla decipiens Sinitshenkova, sp. nov.

Etymology. The Latin *decipiens* (misleading).

Holotype. PIN, no. 3840/1605, part and counterpart of forewing fragment; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 81c, 81d). Adult. In the forewing, SC joins R at the level of r–rs; c-sc joins C considerably proximal to the apex of SC; the preserved fragment of the costal space lacks distinct crossveins; three oblique crossveins are present in the darkened pterostigma. R is curved where it reaches the wing margin. The RS pedicel is somewhat shorter than the posterior branch of RS; the segment of the anterior branch of RS is somewhat longer than the fork of RS;

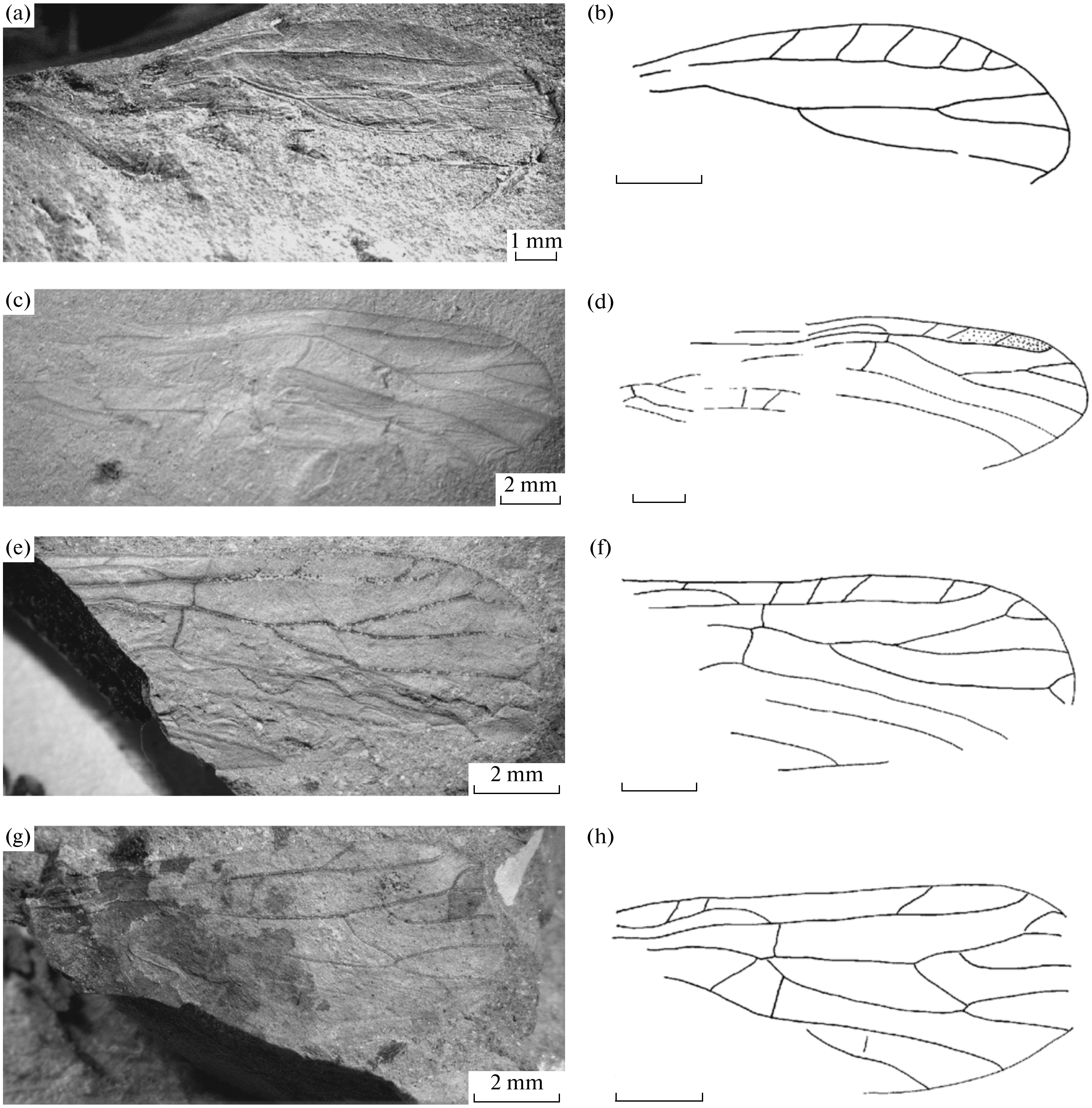

Fig. 81. Stoneflies of the infraorder Perlomorpha, Isady locality, Vologda Region; Severodvinian Stage: (a, b) *Properla issadensis* sp. nov., holotype PIN, no. 3840/425, wing fragment; (c, d) *Kargaloperla decipiens* sp. nov., holotype PIN, no. 3840/1605, forewing fragment; (e, f) *K. furcata* sp. nov., holotype PIN, no. 3840/1606, forewing fragment; (g, h) *Mirumoperla multinerva* gen. et sp. nov., holotype PIN, no. 3840/1614, forewing fragment. Scale bars in Figs. 81–85, 2 mm.

rs–m diverges from RS significantly proximal to r–rs and joins MA markedly distal to its base. The apices of MA and MP slightly diverge where they reach the wing margin.

Measurements, mm. Length of forewing fragment, 18.2; total forewing length, about 21.

Comparison. The relative positions of the apices of SC, r–rs, and rs–m make *K. decipiens* similar to *K. avulsa* Sinitshenkova, 1987, from which the new species is clearly distinguished by the longer pedicel of RS and larger size.

Material. Holotype.

Kargaloperla furcata Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *furcatus* (forked).

Holotype. PIN, no. 3840/1606, part and counterpart of forewing fragment; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 81e, 81f). Adult. In the forewing, SC joins R markedly proximal to r–rs and somewhat proximal to rs–m. Three crossveins are present in the pterostigmal area. R is curved apically, where it reaches the wing margin. The posterior branch of RS is almost four times longer than the pedicel of RS; the fork of the anterior branch of RS is long; the anterior and posterior branches of RS have short forks near the wing margin; rs–m diverges from RS noticeably proximal to r–rs and joins MA noticeably distal to its base. Branches of M only slightly diverge where they reach the wing margin.

Measurements, mm. Length of forewing fragment, 12.1; total forewing length, about 18.

Comparison. The new species is clearly distinguished from all congeners by the proximal position of the apex of SC, the presence of short forks in the branches of RS, and the larger size.

Material. Holotype.

Perlomorpha incertae familiae

Genus *Mirumoperla* Sinitshenkova, gen. nov.

Etymology. From the Latin *mirum* (neutral form of *mirus,* strange) and the generic name *Perla.*

Type species. *M. multinerva* Sinitshenkova, sp. nov.

Diagnosis. Adult. In forewing, SC long; RS dichotomizing twice; M divided distally; additional crossveins present between branches of RS and between RS and M.

Remarks. The unusual, almost dichotomous division of the branches of RS, drawn together by a long oblique crossvein in the apical one-third of the wing, give no reason to consider the new genus close to any known stonefly family. It is not expedient to establish a new family based on one wing fragment; therefore, the family placement of this genus remains uncertain.

Species composition. Type species.

Mirumoperla multinerva Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *multinervus* (multi-nerve).

Holotype. PIN, no. 3840/1614, part and counterpart of forewing fragment; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 81g, 81h). Adult. In the forewing, R is slightly curved where it reaches the wing margin; SC joins R at the level of r–rs; the short c-sc is oblique, joins C noticeably proximal to the SC apex. A distinct oblique crossvein is present in the pterostigmal area. The anterior branch of RS has a short fork near the wing margin, so that RS reaches the wing margin in five branches; r–rs diverges from R almost at the level of the SC apex and flows into RS slightly distal to its first bifurcation, so that the pedicel of RS is absent. One crossvein rs–m diverges from RS somewhat proximal, and another is markedly distal to the first bifurcation of RS. A long, curved crossvein diverges from the anterior branch of RS considerably proximal to its bifurcation and joins the distal branch of RS somewhat distal to its bifurcation. M branches markedly distal to the first bifurcation of RS.

Measurements, mm. Length of forewing fragment, 11.0; total forewing length, about 15.

Material. Holotype.

Suborder Nemourina Newman, 1853

Family Palaeonemouridae Sharov, 1961

Genus *Palaeonemoura* Sharov, 1961

Type species. *P. clara* Sharov, 1961; Kuznetsk Basin; Upper Permian.

Species composition. In addition to the type species, two new and 13 previously described species.

Palaeonemoura antrorsa Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *antrorsus* (directed forward).

Holotype. PIN, no. 3840/495, almost complete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 82a, 82b). Adult. In the forewing, SC joins R at the level of r–rs; c-sc is long, joins C almost at the level of the SC apex; a distinct oblique crossvein is present in the pterostigmal area; the pterostigma is darkened. The fork of RS is almost thrice as long as the pedicel of RS; rs–m diverges from RS noticeably proximal to r–rs and joins MA at a considerable distance from its base. CuA branches markedly distal to the bifurcation of M; m–cu connects the base of MP and the stem of CuA markedly proximal to the bifurcation of CuA. The fork of CuA is short; its anterior branch is almost 2.5 as long as its posterior branch; CuP is short and straight, reaches the wing margin noticeably proximal to the point of M branching; the fork of A_1 is narrow. The veins are pigmented dark brown; a darkened aureole is seen around them.

Measurements, mm. Forewing length, 9.5; maximum width, 3.2.

Comparison. The new species is close to *P. issadensis* Sinitshenkova et Aristov, 2010 and is distinguished from it by the longer pedicel of RS.

Remarks. It is clearly visible in the holotype that RS has an additional branch diverging from RS between r–rs and rs–m and running close to MA without joining it. There is no doubt that this venation pattern is an aberration rather than a species-rank character ; therefore, this character is not included in the description of the species.

Material. Holotype.

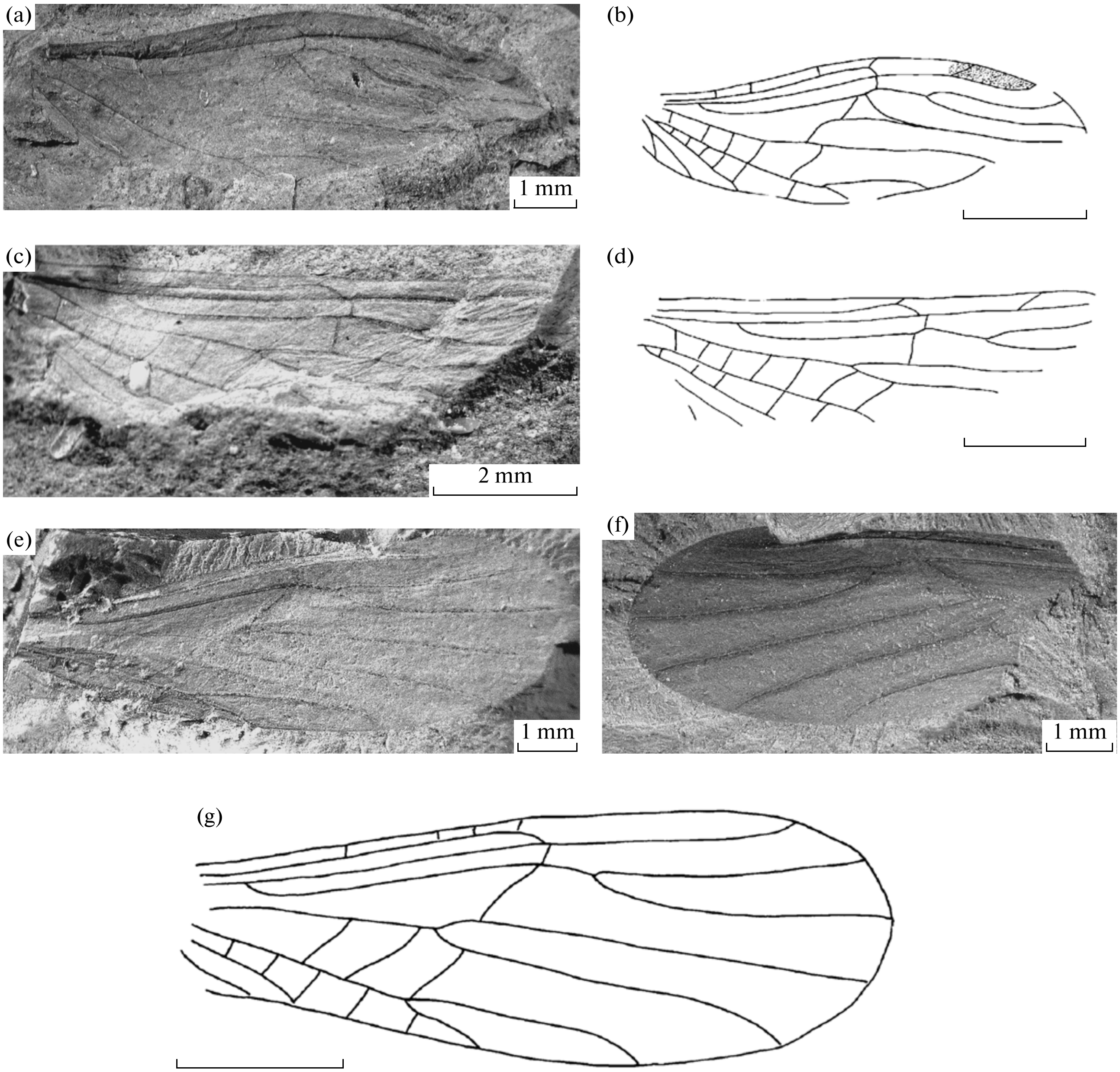

Fig. 82. Stoneflies of the genus *Palaeonemoura*: (a–d) Isady locality, Vologda Region; Severodvinian Stage: (a, b) *P. antrorsa* sp. nov., holotype PIN, no. 3840/495, forewing; (c, d) *P. amica* sp. nov., holotype PIN, no. 3840/1604, forewing fragment; (e–g) *P. repleta* sp. nov., holotype PIN, no. 3286/128, forewing, Chepanikha locality, Udmurtia; Urzhumian Stage.

Palaeonemoura amica Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *amicus* (friendly).

Holotype. PIN, no. 3840/1604, part and counterpart of large forewing fragment, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 82c, 82d). Adult. The anterior margin of the forewing is almost straight; SC joins R somewhat proximal to r–rs; c-sc is short, joins C proximal to the SC apex; one thin oblique crossvein is present in the pterostigmal area; three crossveins are in the costal space. RS smoothly diverges from R in the basal quarter of the wing and, within the segment from the base to r–rs, runs parallel to R; the pedicel of RS is thrice as long as r–rs; rs–m diverges from RS noticeably proximal to r–rs, at the level of the apex of SC and joins MA at a considerable distance from its base; the fork of M is sharp and narrow; the apices of MA and MP slightly diverge near the wing margin. The distal part of CuA is not preserved; CuP is almost straight.

Measurements, mm. Length of forewing fragment, 7.8; total forewing length, about 9.

Comparison. The presence of a crossvein in the pterostigmal area, the proximal position of rs–m, and narrow fork of the media make the new species close to *M. issadensis,* from which it is clearly distinguished by the position of the SC apex proximal to r–rs and by the longer pedicel of RS.

Material. Holotype.

Palaeonemoura repleta Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *repletus* (full).

Holotype. PIN, no. 3286/128, part and counterpart of almost complete wing, well preserved; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 82e–82g). Adult. In the forewing, SC joins R somewhat proximal to r–rs; c-sc is short, joins C noticeably proximal to the SC apex. The apex of SC and r–rs are located in the apical half of the wing; a crossvein in the pterostigmal area of the wing is absent. The branches of RS diverge where they reach the wing margin. The crossvein r–rs is almost vertical; rs–m is strongly oblique, diverges from RS almost at the level of r–rs and joins RS at a considerable distance from the base of MA. CuA branches almost at the level of the division of M, has a wide fork, the anterior branch of which is almost 2.5 as long as the posterior branch; CuP is short, simple, reaches the wing margin noticeably proximal to the bifurcations of M and CuA; the preserved part of A_1 is represented by a straight short vein.

Measurements, mm. Length of forewing fragment, 9.5; total forewing length, about 10; maximum width, 3.3.

Comparison. In the relative positions of the SC apex, r–rs, and rs–m, *P. repleta* is close to *P. issadensis* Sinitshenkova et Aristov, 2010 and is clearly distinguished from it by the absence of a crossvein in the pterostigmal area of the wing and by the branches of RS diverging near the wing margin.

Material. Holotype.

Genus *Palaeotaeniopteryx* Sharov, 1961

Type species. *P. elegans* Sharov, 1961; Upper Permian, Kuznetsk Basin.

Species composition. In addition to the type species, five new and four previously described species.

Palaeotaeniopteryx laeta Sinitshenkova et Aristov, 2010

Palaeotaeniopteryx laeta Sinitshenkova et Aristov, 2010, p. 48, text-figs. 1f–1i.

Holotype. PIN, no. 3840/344, impression of forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Fig. 83a). Adult. In the forewing, SC is short, joins R proximal to r–rs; c-sc is short, joins C somewhat proximal to the SC apex. Two additional crossveins are present in the narrow costal space; two oblique crossveins are present in the darkened pterostigmal area. The pedicel of RS is almost as long as the fork of RS; rs–m joins RS proximal to r–rs. M branches markedly proximal to r–rs and somewhat proximal to the branching of CuA; rs–m diverges from RS somewhat proximal to r–rs and joins MA at a considerable distance from the base of MA. The crossvein m–cu joins the bifurcations of M and CuA. At least four crossveins are present between M and CuA. The fork of CuA is short; its anterior branch flows into the wing margin somewhat distal to r–rs.

Measurements, mm. Forewing length, 12–13.

Remarks. In the original description of the species, data on the morphology of M are absent, because the middle of the wing has not been preserved in the holotype (PIN, no. 3840/344). A well-preserved specimen (PIN, no. 3840/631) found among recently collected materials, allowed the description of the species to be supplemented.

Material. In addition to the holotype, two specimens PIN, nos. 3840/489 and 631, forewing fragments from the same locality.

Palaeotaeniopteryx dejecta Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *dejectus* (fall off).

Holotype. PIN, no. 3840/636, forewing fragment without cubital part; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 83b, 83c). Adult. In the forewing, SC joins R almost at the level of r–rs; c-sc is short, joins C somewhat proximal to the apex of SC. Four crossveins are seen in the costal space; r–rs is very short, less than half as long as rs–m; the fork of RS is narrow, somewhat longer than the pedicel of RS. M branches distal to rs–m, which diverges from RS at the level of r–rs. At least four crossveins are present in the medial space; at least three crossveins are in the cubital space.

Measurements, mm. Forewing length, 9.8.

Comparison. The new species markedly differs from all previously known and newly described below congeners in the M branching distal to rs–m.

Material. Holotype.

Palaeotaeniopteryx constricta Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *constrictus* (contracted).

Holotype. PIN, no. 3840/515, part and counterpart of forewing without basal cubital and anal parts; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 83d, 83e). Adult. In the forewing, SC joins R at the level of r–rs; c-sc is short, joins C somewhat proximal to the apex of SC. R reaches the wing margin curving apically anteriad. The darkened pterostigmal area contains one thin oblique crossvein. RS diverges from R in the basal one-

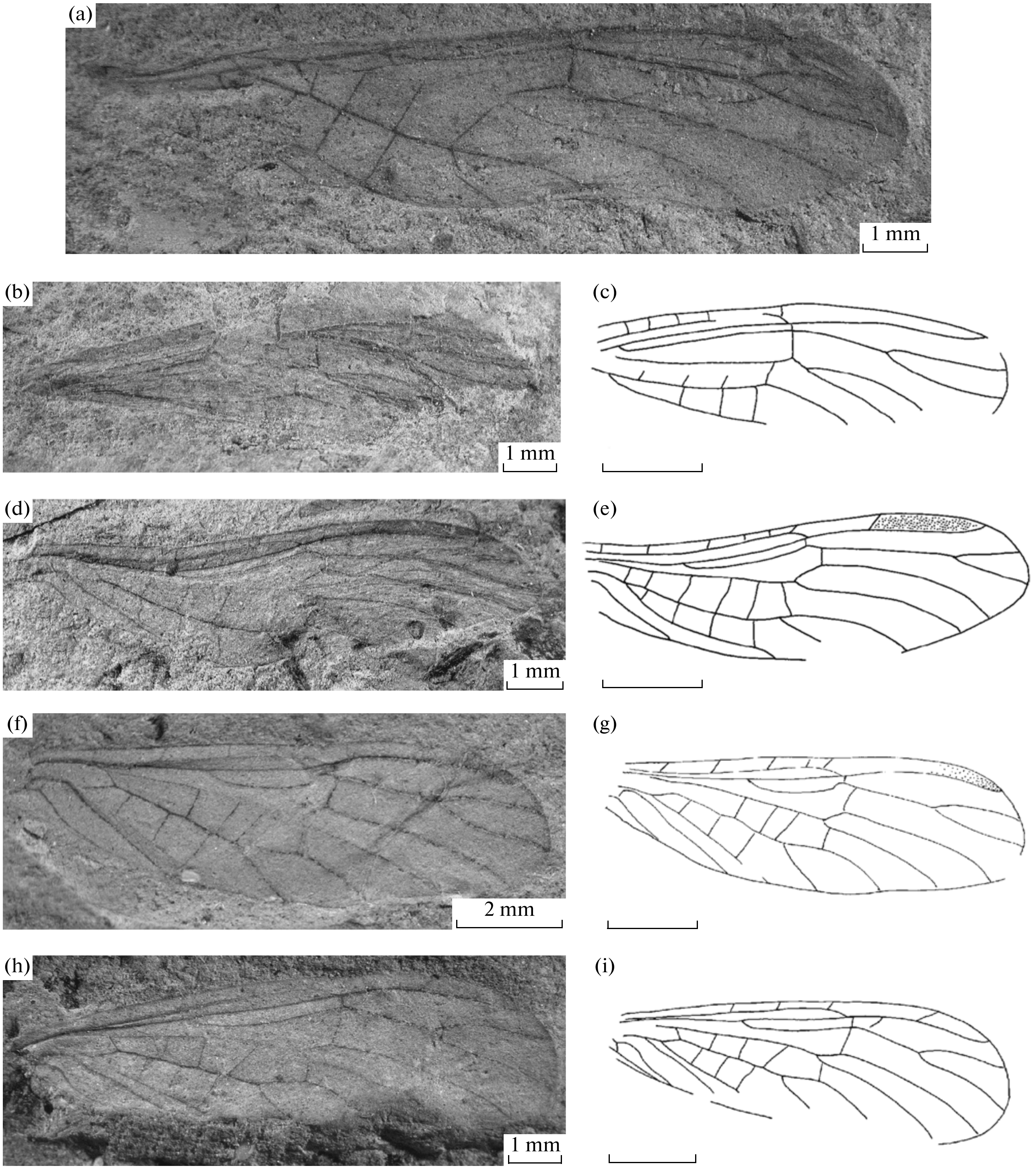

Fig. 83. Stoneflies of the genus *Palaeotaeniopteryx,* Isady locality, Vologda Region; Severodvinian Stage: (a) *P. laeta,* specimen PIN, no. 3840/631, forewing; (b, c) *P. dejecta* sp. nov., holotype PIN, no. 3840/636, forewing fragment; (d, e) *P. constricta* sp. nov., holotype PIN, no. 3840/515, forewing fragment; (e, g) *P. adjecta* sp. nov., holotype PIN, no. 3840/1611, forewing; (h, i) *P. succida* sp. nov., holotype PIN, no. 3840/606, forewing fragment.

third of the wing; the pedicel of RS is almost thrice as long as the fork of RS; branches of the fork diverge towards the wing margin. M branches somewhat proximal to r–rs; rs–m is somewhat longer than r–rs and diverges from the RS pedicel considerably distal to r–rs; MA and MP are almost parallel. CuA branches somewhat proximal to the division of M; CuP is curved, reaches the wing margin almost at the level of the CuA division. A_1 is long, slightly sinuous. Six crossveins are present in the medial space and four crossveins are in the cubital space.

Measurements, mm. Forewing length, 10.

Comparison. The new species markedly differs from all previously known and newly described congeners in the considerably more distal position of rs–m relative to r–rs.

Material. Holotype.

Palaeotaeniopteryx adjecta Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *adjectus* (adjoining).

Holotype. PIN, no. 3840/1611, part and counterpart of forewing, very well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 83f, 83g). Adult. In the forewing, SC joins R somewhat proximal to r–rs; c-sc joins C proximal to the apex of SC. Four crossveins are present in the costal space; crossveins are absent in the darkened pterostigmal area. R is slightly curved apically where it reaches the wing margin. RS is short, diverges from R somewhat distal to the basal one-third of the wing, smoothly curved in the segment between its base and r–rs; r–rs is short, less than half as long as rs–m. The pedicel of RS is subequal to (holotype), or somewhat longer than (paratype) the fork of RS, which is weakly widened near the wing margin; rs–m is straight, diverges from RS noticeably distal to r–rs and joins MA markedly distal to the base of MA; MP is slightly curved. CuA branches somewhat proximal to the fork of M; the branches of CuA broadly diverge near the wing margin; CuP joins the wing margin almost at the level of the bifurcation of CuA; A_1 is almost straight; A_2 is simple, smoothly curved towards the posterior wing margin. The wing is 3.3 times as long as its maximum width.

Measurements, mm. Forewing length, 10.1; maximum width, 3.0.

Comparison. In the distal position of rs–m, *P. adjecta* is close to *P. constricta* and differs from it in the straight anterior margin of the forewing, the shorter fork of RS, and the absence of a crossvein in the pterostigmal area.

Material. In addition to the holotype, paratype no. 3840/490, part and counterpart of a well-preserved almost complete forewing, without its basal part in a piece of rock with an oblique transverse crack.

Palaeotaeniopteryx succida Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *succidus* (juicy).

Holotype. PIN, no. 3840/606, part and counterpart of almost complete forewing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 83h, 83i). Adult. In the forewing, SC joins R noticeably proximal to r–rs; c-sc is distinct, reaches the wing margin markedly proximal to the apex of SC. Two short crossveins are seen in the costal space; one thin oblique crossvein is present in the pterostigmal area. R reaches the wing margin slightly curving. RS diverges from R at the base of the middle one-third of the wing; r–rs is short, less than half as long as rs–m. An additional oblique r–rs is present distal to the first r–rs; the pedicel of RS is almost subequal in length to the fork of RS; rs–m diverges from RS at the level of the first short r–rs, forming together with it a straight line, and joins MA at a considerable distance from the base of MA. M branches noticeably proximal to the apex of SC and somewhat distal to the division of CuA; the branches of M slightly diverge near the wing margin. The fork of CuA is wide; m–cu diverges from the base of MP noticeably proximal to rs–m and joins the anterior branch of CuA at a considerable distance from the base of this branch. CuP is straight; its apex is not preserved; A_1 is straight; A_2 has two branches; the anterior branch is long, strongly curved at the base; the posterior branch is short and straight. Four crossveins are present in the medial space; three are in the cubital space. The veins are brown; the pterostigma is slightly darkened.

Measurements, mm. Forewing length, 10.3.

Comparison. The position of r–rs and rs–m on the same line makes *P. succida* similar to *P. triternata* Sinitshenkova and Aristov, 2010 from Isady; the new species is distinguished from it by the CuA with two branches and the shorter pedicel of RS.

Remarks. The presence of additional oblique r–rs located distal to the first short r–rs is manifestation of random variation of venation; this aberrant feature should not be regarded as a species character. Therefore, the wing impression in specimen PIN, no. 3840/599, which lacks an additional r–rs, but is similar in venation and size (wing is 10.5 mm long), is assigned to this species.

Material. In addition to the holotype, paratype PIN, no. 3840/599, large forewing fragment without the distal r–rs, from the same locality.

Palaeotaeniopteryx amissa Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *amissus* (lost).

Holotype. PIN, 3840/1608, counter impression of complete forewing, very well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 84a, 84b). Adult. In the forewing, SC joins R at the level of r–rs; c-sc is long, diverges from the apex of SC and joins C somewhat distal to its apex. Five additional crossveins are present in the costal space and one oblique crossvein is in the darkened pterostigmal area near the wing apex. The pedicel of RS is somewhat longer than the fork of RS;

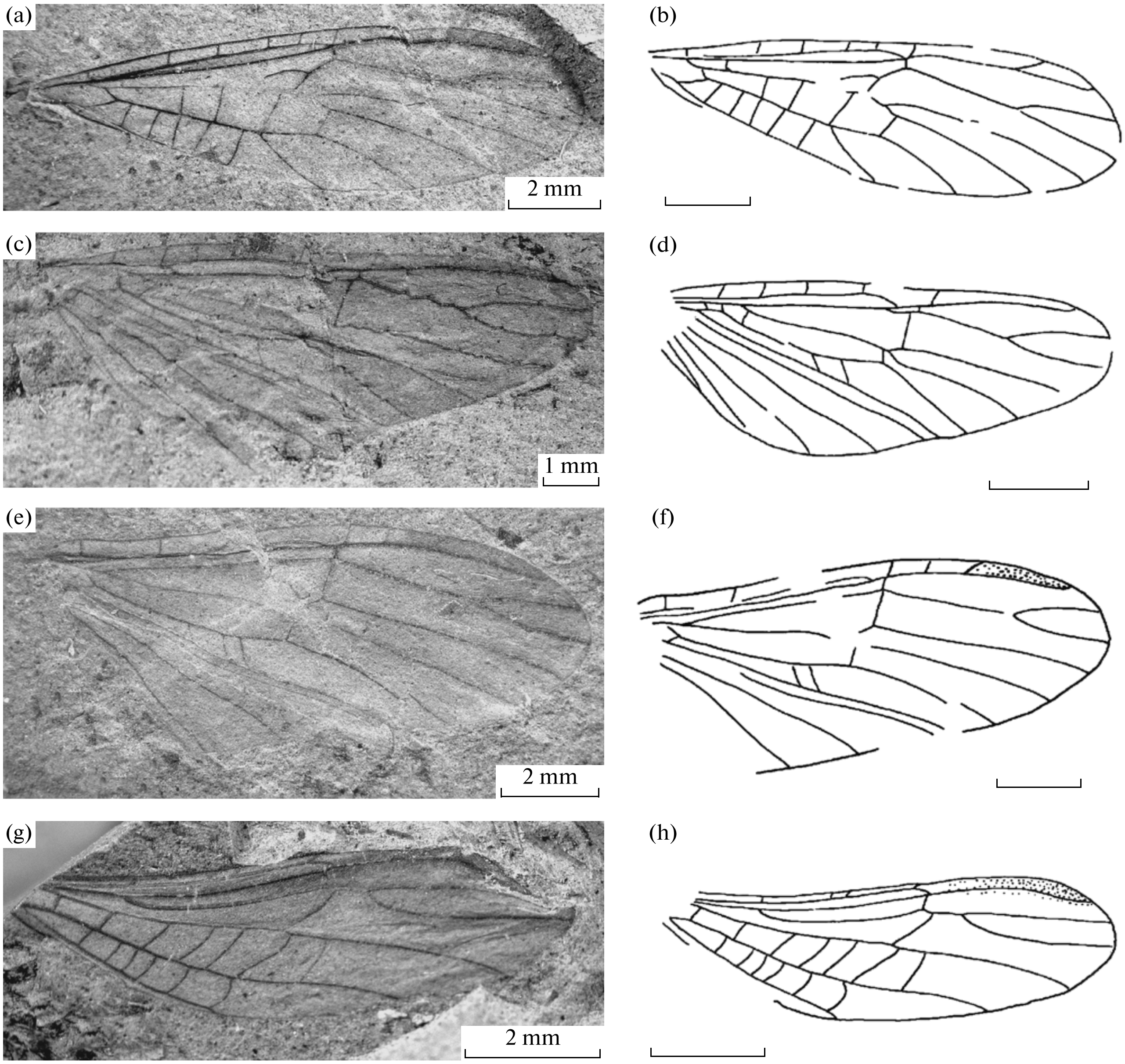

Fig. 84. Stoneflies of the family Palaeonemouridae, Isady locality, Vologda Region; Severodvinian Stage: (a, b) *Palaeotaeniopteryx amissa* sp. nov., holotype PIN, no. 3840/1608, forewing; (c, d) *P. fixa* sp. nov., holotype PIN, no. 3840/605, hindwing; (e, f) *P. mira* sp. nov., holotype PIN, no. 3840/1612, hindwing; (g, h) *Votaknemoura admiranda* gen. et sp. nov., holotype PIN, no. 3840/1607, forewing.

the base of RS is in the shape of a short crossvein joining M somewhat distal to its base; the part of RS basal to r–rs is very distinct; the main part of RS is probably fused with M; at the base of the wing, RS diverges from R and joins the pedicel of M, so that RS is only represented by a short crossvein between R and M. The crossvein rs–m joins RS proximal to r–rs; M branches markedly distal to r–rs and the bifurcation of CuA; rs–m joins M proximal to its bifurcation. The crossvein m–cu connects the bases of MP and CuA. At least four crossveins are present between M and CuA; five crossveins are in the cubital space. The fork of CuA is long; its anterior branch reaches the wing margin markedly distal to r–rs.

Measurements, mm. Forewing length, 12.5; maximum width, 4.7.

Comparison. The new species is similar to *P. laeta* in size and the presence of two crossveins in the pterostigmal area and clearly distinguished by the distal division of M, distal to r–rs; the distal position of the apex of SC, which joins R at the level of r–rs; and by the distinctive position of c-sc, which diverges from the apex of SC.

Remarks. The new species has an abnormal shape of RS, with most of the stem fused with M and only a minor rudiment of the base and a part remaining distal to r–rs. This shape of RS is clearly abnormal; it is found in the fossil record for the first time. More common variants are additional crossveins or somewhat less frequent additional longitudinal veins, which then join the main veins (*Palaeonemoura antrorsa*).

The shape of RS clearly distinguishes the new species from all known Palaeonemouridae, but, in my opinion, a new genus should not be established, because the above characters are considered aberrant.

Material. Holotype.

Palaeotaeniopteryx fixa Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *fixus* (fixed, firm).

Holotype. PIN, no. 3840/605, part and counterpart of complete hindwing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 84c, 84d). Adult. The hindwing has an extended anal area. In the hindwing, SC joins R markedly proximal to r–rs; c-sc is short, reaches the wing margin noticeably proximal to the apex of SC. Three crossveins are present in the costal space; in the pterostigmal area, crossveins are absent. RS diverges from R almost at the level of the middle of the wing, somewhat proximal to the apex of SC; the pedicel of RS is subequal in length to the fork of RS; r–rs is short; rs–m is long, four times as long as r–rs, diverges from RS noticeably proximal to r–rs. M branches significantly proximal to rs–m; CuA and CuP are simple; CuA is drawn close together with MP by a very short crossvein at some distance from the base of MP; CuP is straight. Five almost straight anal veins are present in the expanded anal area.

Measurements, mm. Hindwing length, 10.6; maximum width, 4.0.

Comparison. The short pedicel of RS makes the new species close to *P. elegans* Sharov, 1961, in which the morphology of both forewing and hindwing is known. *P. fixa* is clearly distinguished from *P. elegans* in the proximal position of the apex of SC and rs–m.

Material. Holotype.

Palaeotaeniopteryx mira Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *mirus* (wonderful).

Holotype. PIN, 3840/1612, counter impression of complete hindwing, well preserved; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 84e, 84f). Adult. In the hindwing, SC adjoins R at some distance from the base, then, is separated from it and joins R somewhat proximal to r–rs. Two crossveins are present in the costal space and three are in the darkened pterostigmal area; c-sc is absent. RS is fused with M at the wing base and, then, runs parallel to R. The pedicel of RS is longer than the fork of RS; rs–m diverges from RS at the level of r–rs and joins MA at some distance from the base of MA. CuA is simple, smoothly curved in the apical half; CuP is simple, slightly curved; three simple anal veins are visible in the preserved expanded anal area.

Measurements, mm. Hindwing length, 11.5.

Comparison. The new species is clearly distinguished from *P. elegans* Sharov, 1961 and *P. fixa* sp. nov., in which the hindwing morphology is known, by the long pedicel of RS which is fused with M at the wing base.

Material. Holotype.

Genus *Votaknemoura* Sinitshenkova, gen. nov.

Etymology. A random combination of letters and the generic name *Nemoura*.

Type species. *V. admiranda* Sinitshenkova, sp. nov.

Diagnosis. Adult. Small stonefly. Anterior forewing margin noticeably concave in basal half. Costal space with additional veins; SC more than half as long as wing. RS with two branches; M, CuA, and CuP simple.

Species composition. Type species.

Comparison. The new genus markedly differs from all known genera in the simple M.

Remarks. The considerable oligomerization of forewing venation found in *Votaknemoura* is an apomorphic character, but the presence of additional crossveins in the costal space is evidence of an archaic venation pattern.

Votaknemoura admiranda Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *admirandus* (astonishing).

Holotype. PIN, no. 3840/1607, part and counterpart of almost complete forewing, well preserved, with costal margin somewhat crumpled apically; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 84g, 84h). Adult. In the forewing, C, SC, and R curved, following a concave anterior wing margin in the basal half. Three additional crossveins are present in the costal space; SC joins R noticeably distal to r–rs; c-sc is short, joins C proximal to the apex of SC. The crossvein rs–m is long, oblique, diverges from RS noticeably distal to r–rs and proximal to its division, so that a short pedicel of RS is formed. M is simple, smoothly curved; CuA is smoothly curved in the apical one-third, joins the posterior wing margin somewhat distal to the division of RS. CuP is slightly incurved, reaches the posterior wing margin somewhat proximal to the middle of the wing. Seven crossveins are present in the medial space and six are in the cubital space. The wing is approximately 3.4 times as long as its maximum width.

Measurements, mm. Length of the forewing fragment, 8.4; total forewing length, about 9; maximum width, 2.5.

Material. Holotype.

Genus *Palaeonemourica* Sinitshenkova, 2004

Type species. *P. novojilovi* Sinitshenkova, 2004, Prokoshevo locality, Udmurtia; Tatarian Series, Upper Permian.

Species composition. In addition to the type species, three new species and *P. subita* Sinitshenkova, 2004 from Novo-Aleksandrovka (Orenburg Region).

Palaeonemourica diluta Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *dilutus* (pale).

Holotype. PIN, no. 3840/638, forewing fragment without cubital part; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 85a, 85b). Adult. In the forewing, SC joins R markedly proximal to r–rs; c–r is short, joins C markedly proximal to the apex of SC. In the darkened pterostigmal area, crossveins are absent. RS branches distal to r–rs; the fork in its first branch is long; the wavy rs–m diverges from RS markedly proximal to r–rs, almost at the level of the apex of SC; r–rs is less than half as long as rs–m. The veins are dark brown; the pterostigmal area is brownish.

Measurements, mm. Length of forewing fragment, 7.0; total forewing length, about 8.

Comparison. The new species is clearly distinguished from all congeners by the basal position of the apex of SC and rs–m relative to r–rs.

Material. In addition to the holotype, paratypes PIN, nos. 3840/650 and 658, forewing fragments from the same locality.

Palaeonemourica formalis Sinitshenkova, sp. nov.

Etymology. The Latin *formalis* (formal).

Holotype. PIN, no. 3840/637, part and counterpart of forewing fragment without basal part; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 85c–85e). Adult. In the forewing, SC joins R noticeably proximal to r–rs; c-sc is long, joins C almost at the level of the apex of SC. Three crossveins are visible in the pterostigmal area. The pedicel of RS is slightly shorter than the fork of RS; the anterior branch of RS has a short terminal fork. The bifurcations of RS are wide; r–rs is short; rs–m is long, straight, almost vertical, diverges from RS at the level of r–rs. M branches noticeably proximal to r–rs and rs–m; MP is weakly curved; MA diverges from the stem of M, smoothly curving at the base; the apices of MA and MP broadly diverge towards the wing margin. The crossvein joining M and CuA diverges from MP somewhat distal to the division of M. CuA is long, smoothly curved, reaches the wing margin at the level of the first bifurcation of RS. The longitudinal veins are dark brown; the pterostigmal area is darkened.

Measurements, mm. Length of forewing fragment, 8.0; total forewing length, about 11.

Comparison. In the basal position of the SC apex, *P. formalis* is close to *P. diluta* and is clearly distinguished from it by the long pedicel of RS and the short fork in the anterior branch of RS. It is distinguished from the type species, which also has a short fork in the anterior branch of RS, by the presence of three crossveins in the pterostigmal area and by the smaller size.

Material. Holotype.

Palaeonemourisca strigosa Sinitshenkova, sp. nov.

Etymology. Feminine gender form of the Latin *strigosus* (colorless).

Holotype. PIN, no. 3286/127, part and counterpart of wing fragment; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 85f, 85g). Adult. In the forewing, SC joins R at the level of r–rs; c-sc is long, joins C somewhat distal to the apex of SC; a crossvein in the pterostigmal area of the wing is absent. The branches of RS are almost parallel; the fork in the anterior branch of RS is long; rs–m diverges from RS somewhat proximal to r–rs and joins MA markedly distal to the base of MA. The crossveins and pterostigma are dark brown.

Measurements, mm. Forewing length, 9.8.

Comparison. In the presence of a long fork on the anterior branch of RS, the new species is close to *P. subita* from Novo-Aleksandrovka and to *P. diluta* from Isady. *P. strigosa* is distinguished from the former species by the absence of a crossvein in the pterostigmal area of the wing and from the latter by the distal position of the apex of SC and rs–m and by the larger size.

Material. Holotype.

Key to Stoneflies of the Family Palaeonemouridae Based on Normally Developed Wings

Key to Genera

1 (2) M simple; RS with two branches........................
.................*Votaknemoura* Sinitshenkova, gen. nov.
...................(*V. admiranda* Sinitshenkova, sp. nov.)

2 (1) M divided into MA and MP; RS with two or three branches.

3 (4) RS with three branches; its anterior branch divided...
.................*Palaeonemourisca* Sinitshenkova, 2004.

4 (3) RS has two branches.

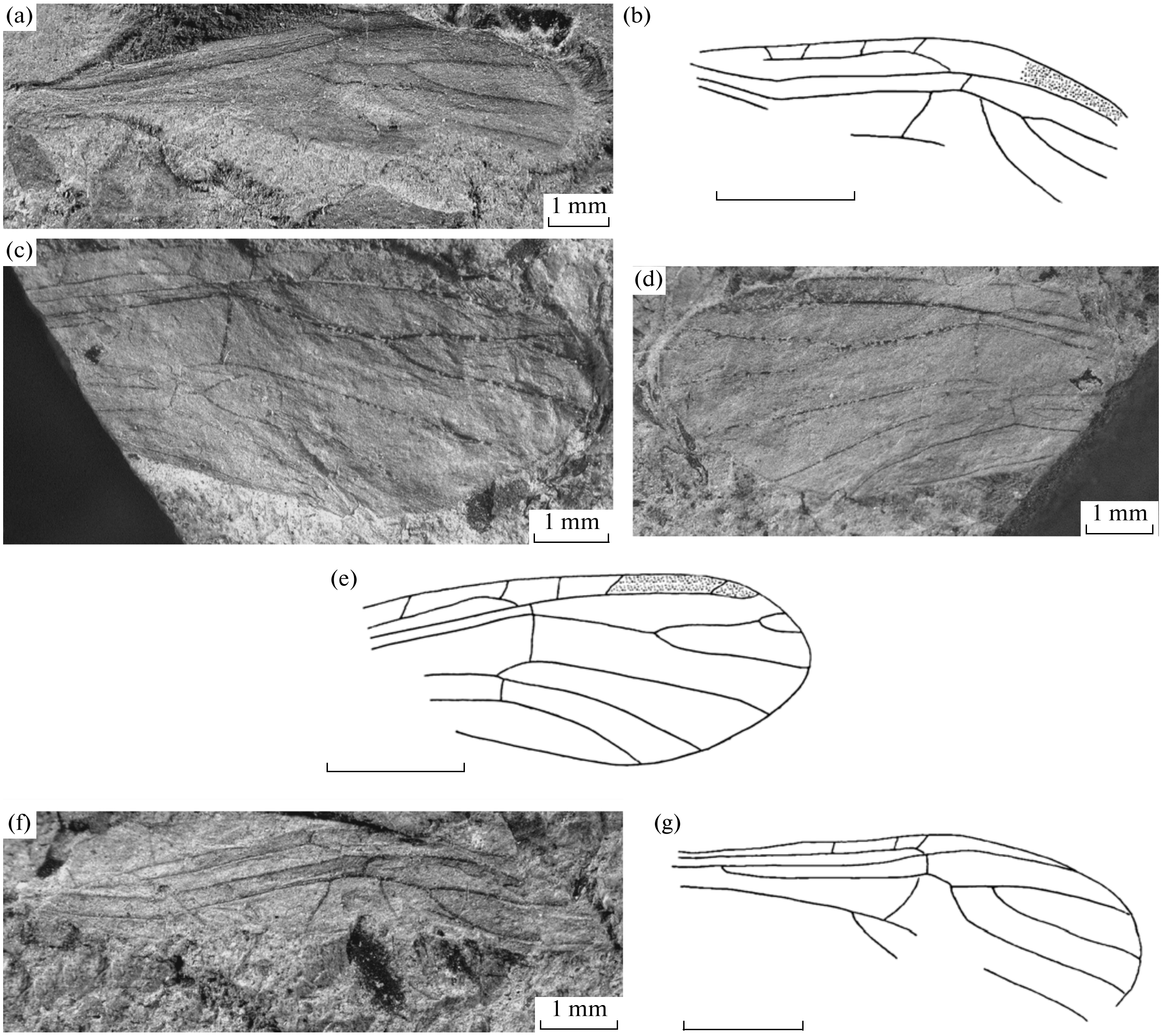

Fig. 85. Stoneflies of the genus *Palaeonemourisca*: (a–e) Isady locality, Vologda Region; Severodvinian Stage: (a, b) *P. diluta* sp. nov., holotype PIN, no. 3840/638, forewing fragment; (c–e) *P. formalis* sp. nov., holotype PIN, no. 3840/637, forewing fragment; (f, g) *P. strigosa* sp. nov., holotype PIN, no. 3286/127, forewing fragment; Chepanikha locality, Urzhumian Stage of Udmurtia.

5 (6) Pedicel of RS short, markedly shorter than fork of RS.. ....*Palaeonemoura* Sharov, 1961.

6 (5) Pedicel of RS long, markedly longer than, or equal in length to, fork of RS............................... ....*Palaeotaenipteryx* Sharov, 1961.

Key to Species of the Genus Palaeonemourisca Sinitshenkova, 2004

1 (4) Pterostigmal area with crossveins.

2 (3) Pterostigmal area with one long crossvein. Fork in anterior branch of RS long. Wing about 11 mm long. Novo-Aleksandrovka.................................. ....*P. subita* Sinitshenkova, 2004.

3 (2) Pterostigmal area with four crossveins. Fork in anterior branch of RS short. Wing about 11 mm long. Isady.. ....*P. formalis* Sinitshenkova, sp. nov.

4 (1) Pterostigmal area without crossveins.

5 (6) Fork in anterior branch of RS short. Wing about 13 mm long. Prokoshevo..................................... ....*P. novojilovi* Sinitshenkova, 2004.

6 (5) Fork in anterior branch of RS long.

7 (8) SC joining R markedly proximal to r–rs; c-sc joining C proximal to apex of SC. Wing about 8 mm long. Isady.. ....*P. diluta* Sinitshenkova, sp. nov.

8 (7) SC joining R at level of r–rs; c-sc joining C almost at level of apex of SC. Wing 9.8 mm long. Chepanikha.. *P. strigosa* Sinitshenkova, sp. nov.

Key to Species of the Genus Palaeonemoura Sharov, 1961

1 (24) Pterostigmal area with crossveins.

2 (5) Pterostigmal area with two crossveins.

3 (4) Two rs–m present. Wing about 5.5 mm long. Bor-Tologoi.. *P. finitima* Sinitshenkova, 1992.

4 (3) One rs–m present. Wing 9–10 mm long. Karaungir-II... *P. zwicki* Sinitshenkova, 1987.

5 (2) Pterostigmal area with one crossvein.

6 (7) Two rs–m present. Wing 8.4 mm long. Kaltan... *P. altaica* Sharov, 1962.

7 (6) One rs–m present.

8 (9) Crossvein c-sc long, joining C distal to SC apex. Wing 13 mm long. Novo-Aleksandrovka.. *P. lepida* Sinitshenkova, 2004.

9 (8) Crossvein c-sc short, joining C proximal to, or almost at level of, SC apex.

10 (21) Crossvein rs–m almost twice as long as r–rs.

11 (18) Crossvein rs–m diverging from RS proximal to r–rs.

12 (17) Crossvein c-sc joining C proximal to of SC apex.

13 (14) Crossvein c-sc joining C considerably proximal to apex of SC. Wing 11–12 mm long. Galevo....................................... *P. abdita* Sinitshenkova, 2004.

14 (13) Crossvein c-sc joining C significantly proximal to apex of SC.

15 (16) Pedicel of RS twice as long as r–rs. Wing about 8 mm long. Isady.. *P. issadensis* Sinitshenkova et Aristov, 2010.

16 (15) Pedicel of RS thrice as long as r–rs. Wing about 9 mm long. Isady... *P. amica* Sinitshenkova, sp. nov.

17 (12) Crossvein c-sc joining C at level of apex of SC. Isady.. *P. antrorsa* Sinitshenkova, sp. nov.

18 (11) Crossvein rs–m diverging from RS at level of r–rs.

19 (20) SC joining R at level of r–rs. Anterior branch of CuA long, smoothly curved. Wing 6.5 mm long. Novo-Aleksandrovka.. *P. petaloidea* Sinitshenkova, 2004.

20 (19) SC joining R proximal to r–rs. CuA with short fork. Wing 8.3 mm long. Kaltan.. *P. clara* Sharov, 1961.

21 (10) Crossvein rs–m somewhat longer than r–rs.

22 (23) Crossvein rs–m diverging from RS at level of r–rs. Forks of RS and M rounded. Fork of CuA wide. Wing 8 mm long. Novo-Aleksandrovka... *P. riparia* Sinitshenkova, 2004.

23 (22) Crossvein rs–m diverging from RS proximal to r–rs. Forks of RS and M acute. Wing about 9 mm long. Novo-Aleksandrovka... *P. remota* Sinitshenkova, 2004.

24 (1) Pterostigmal area without crossveins.

25 (26) SC joining R somewhat distal to r–rs; rs–m diverging from RS significantly distal to rs–m. Wing 9.2 mm long. Novo-Aleksandrovka.. *P. apicalis* Sinitshenkova, 2004.

26 (25) SC joining R at level of, or proximal to, r–rs; rs–m diverging from RS proximal to, or at level of, r–rs.

27 (28) SC joining R considerably proximal to r–rs. Wing 8.3 mm long. Chepanikha... *P. proximalis* Sinitshenkova, 2004.

28 (27) SC joining R at level, or almost at level, of r–rs.

29 (30) Crossvein rs–m forms straight line with r–rs. Wing about 10 mm long. Galevo... *P. furcata* Sinitshenkova, 2004.

30 (29) Crossvein rs–m diverging from RS proximal to r–rs

31 (32) Crossvein rs–m almost vertical; M branching somewhat proximal to r–rs. Wing about 7 mm long. Novo-Aleksandrovka.. *P. duplicata* Sinitshenkova, 2004.

32 (31) Crossvein rs–m oblique; M branching considerably proximal to r–rs. Wing about 10 mm long. Chepanikha... *P. repleta* Sinitshenkova, sp. nov.

Key to Species of the Genus Palaeotaenipteryx Sharov, 1961

1 (6) Hindwing.

2 (5) Stem of RS long, diverging from R at wing base, fused there with M; rs–m diverging from R at level of r–rs.

3 (4) Apex of SC considerably distal to r–rs. Wing 6.3 mm long. Kaltan.. *P. elegans* Sharov, 1961.

4 (3) Apex of SC considerably proximal to r–rs. Wing 11.5 mm long. Isady.. *P. mira* Sinitshenkova, sp. nov.

5 (2) Stem of RS shorter, diverging from R in basal one-third of wing; rs–m diverging from R proximal to r–rs. Wing 10.6 mm long. Isady.. *P. fixa* Sinitshenkova, sp. nov.

6 (1) Forewing.

7 (14) Pterostigmal area without crossveins.

8 (9) CuA with three branches; rs–m and r–rs forming one straight line. Wing 10.5 mm long. Isady...................... *P. triternata* Sinitshenkova et Aristov, 2010.

9 (8) CuA with two branches; rs–m positioned distal or proximal to r–rs.

10 (11) SC joining R distal to r–rs. Wing about 7 mm long. Novo-Aleksandrovka.................................. ....*P. distalis* Sinitshenkova, 2004.

11 (10) SC joining R proximal to, or almost at level of, r–rs.

12 (13) rs–m positioned distal to r–rs; M branching somewhat proximal to r–rs. Wing about 9 mm long. Isady.. ....*P. adjecta* Sinitshenkova, sp. nov.

13 (12) rs–m diverging from R at level of r–rs; M branching significantly distal to r–rs. Wing about 9.8 mm long. Isady..................................... ....*P. dejecta* Sinitshenkova, sp. nov.

14 (7) Pterostigmal area with one or two crossveins.

15 (16) Crossvein rs–m positioned distal to r–rs. Wing about 9.8 mm long. Isady...................................... ....*P. constricta* Sinitshenkova, sp. nov.

16 (15) Crossvein rs–m positioned proximal to, or at level of, r–rs.

17 (18) Pterostigmal area with two crossveins. Wing about 12 mm long. Isady...................................... ....*P. laeta* Sinitshenkova et Aristov, 2010.

18 (17) Pterostigmal area with one crossvein.

19 (20) M with three branches. Wing about 6 mm long. Novo-Aleksandrovka... ....*P. perlonga* Sinitshenkova, 2004.

20 (19) M with two branches.

21 (22) Crossvein rs–m diverging from R at level of r–rs. Wing 10.3 mm long. Isady.................................... ....*P. succida* Sinitshenkova, sp. nov.

22 (21) Crossvein rs–m diverging from R considerably proximal to r–rs.

23 (24) Wing about 6.5 mm long. Kaltan.................... ....*P. elegans* Sharov, 1961.

24 (23) Wing 12.5 mm long. Isady............................. ....*P. amissa* Sinitshenkova, sp. nov.

2.8. New Taxa of the Superorder Orthopteroidea from the Latter Half of the Permian of European Russia

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In this study, new certain and possible members of the orders Titanoptera, Orthoptera, and Phasmatoptera from the Middle Permian of Udmurtia and Late Permian of Vologda, Orenburg, and Vladimir Regions are described: *Monstrotitan monstrosus* gen. et sp. nov. (Deinotitanidae stat. nov.); *Meselcana udmurtica* sp. nov., and *M. vologodica* sp. nov. (Permelcanidae: Meselcaninae); *Suchonoedischia incompleta* gen. et sp. nov. (Pruvostitidae: ?Pruvostitinae); *Archifergania isadyensis* gen. et sp. nov. (Proparagryllacrididae: Kashgarlimahmutiinae); *Isadyphasma bashkuevi* gen. et sp. nov., *I. suchonae* sp. nov., and *I. deminutum* sp. nov. (?Permophasmatidae). The Triassic subfamily Meselcaninae and the genus *Meselcana* are recorded in the Middle and Upper Permian; the Triassic family Proparagryllacrididae and subfamily Kashgarlimahmutiinae and several groups unknown from deposits later than the Middle Permian (the family Oedischiidae, subfamily Tcholmanvissinae and, possibly, the subfamily Pruvostitinae) are recorded in the Upper Permian. In addition, the forewing morphology is described for the first time in possible members of the Late Permian family Permophasmatidae, known previously only from a small fragment.

The superorder Orthopteroidea belongs to the infraorder Polyneoptera and comprises three orders. The order Titanoptera is presumably known beginning from the Middle Carboniferous to the Middle or Late Triassic and is possibly ancestral to two other orders: Orthoptera, the earliest known record of which comes from the Late Carboniferous; and Phasmatoptera, the earliest known record of which is probably also Late Carboniferous (Gorochov, 2001, 2004).

The material described here comes from four European Russian localities of the latter half of the Permian:

1. Chepanikha. Udmurtia, Zavyalovskii District, Rossokha River Valley, 1.8 km north of the village of Chepanikha; Middle Permian, Urzhumian Stage.

2. Novo-Aleksandrovka. Orenburg Region, Tyulganskii District, 6 km north of the village of Troitskoe; Upper Permian, Severodvinian Stage, Vyazovka Formation.

3. Isady (=Mutovino). Vologda Region, Velikoustyugskii District, left bank of the Sukhona River (1.8 km downstream from Mutovino) opposite the village of Isady; Upper Permian, Severodvinian Stage, Upper Severodvinian Substage, Poldarsa Formation, lower part of the Kalikino Member.

4. Balymotikha. Vladimir Region, southern outskirts of the town of Vyazniki, east of the village of Balymotikha, left margin of gully near the point where it is crossed by highway; Upper Permian, Vyatkian Stage, Upper Vyatkian Substage, Zhukovian Horizon.

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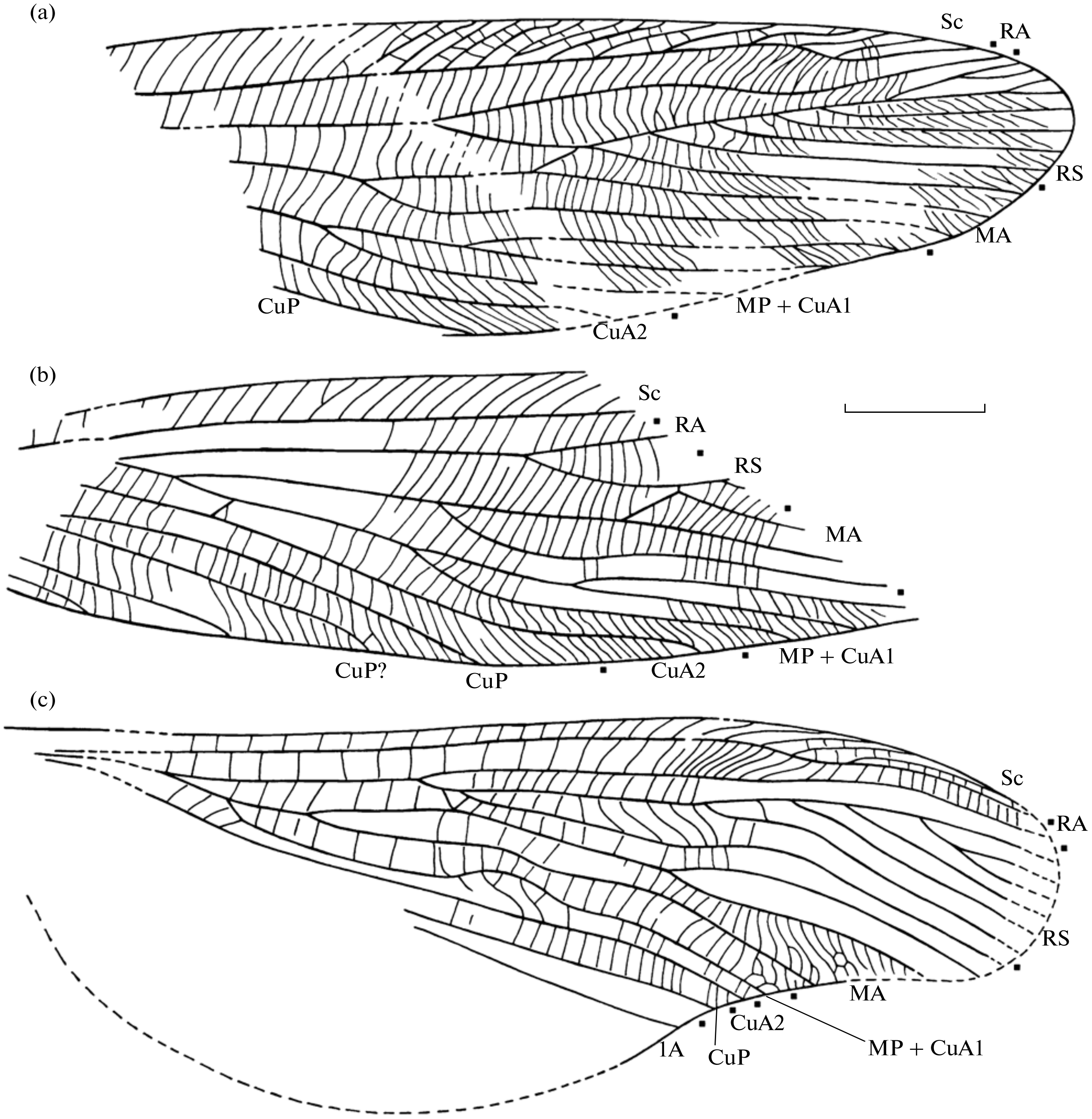


Fig. 86. Impressions possibly belonging to *Monstrotitan monstrosus* gen. et sp. nov. (Deinotitanidae), Isady locality, of Vologda Region; Severodvinian Stage: (a) PIN, no. 3840/655, forewing without proximal portion; (b) PIN, no. 3840/660, forewing without distal portion; (c) PIN, no. 3840/1217, possibly, female hindwing without anal fan. Scale bar in Figs. 86–89, 5 mm.

?Order Titanoptera Sharov, 1968

Family Deinotitanidae (Gorochov, 2007), stat. nov.

Deinotitaninae: Gorochov, 2007b, p. 32.

Type genus. *Deinotitan* Gorochov, 2007.

Diagnosis (Figs. 86a–86c; 87a, 87b). Wings (probably hindwings and possibly only in male) with stridulatory apparatus, in which parts of areas between RS and MA, between branches of MA, and between MA and MP+CuA1 dilated (these parts are probably the main sound-producing areas, which can sometimes also include some other dilated areas, e.g., the area between RA and RS); stem of Sc (probably in both pairs of wings in both sexes) with S-shaped curve in distal half, and with distal branches almost longitudinal and generally longer than its other branches.

Generic composition. *Deinotitan* Gorochov, 2007 from the Upper Permian of the Orenburg Region (new interpretation of its venation is shown

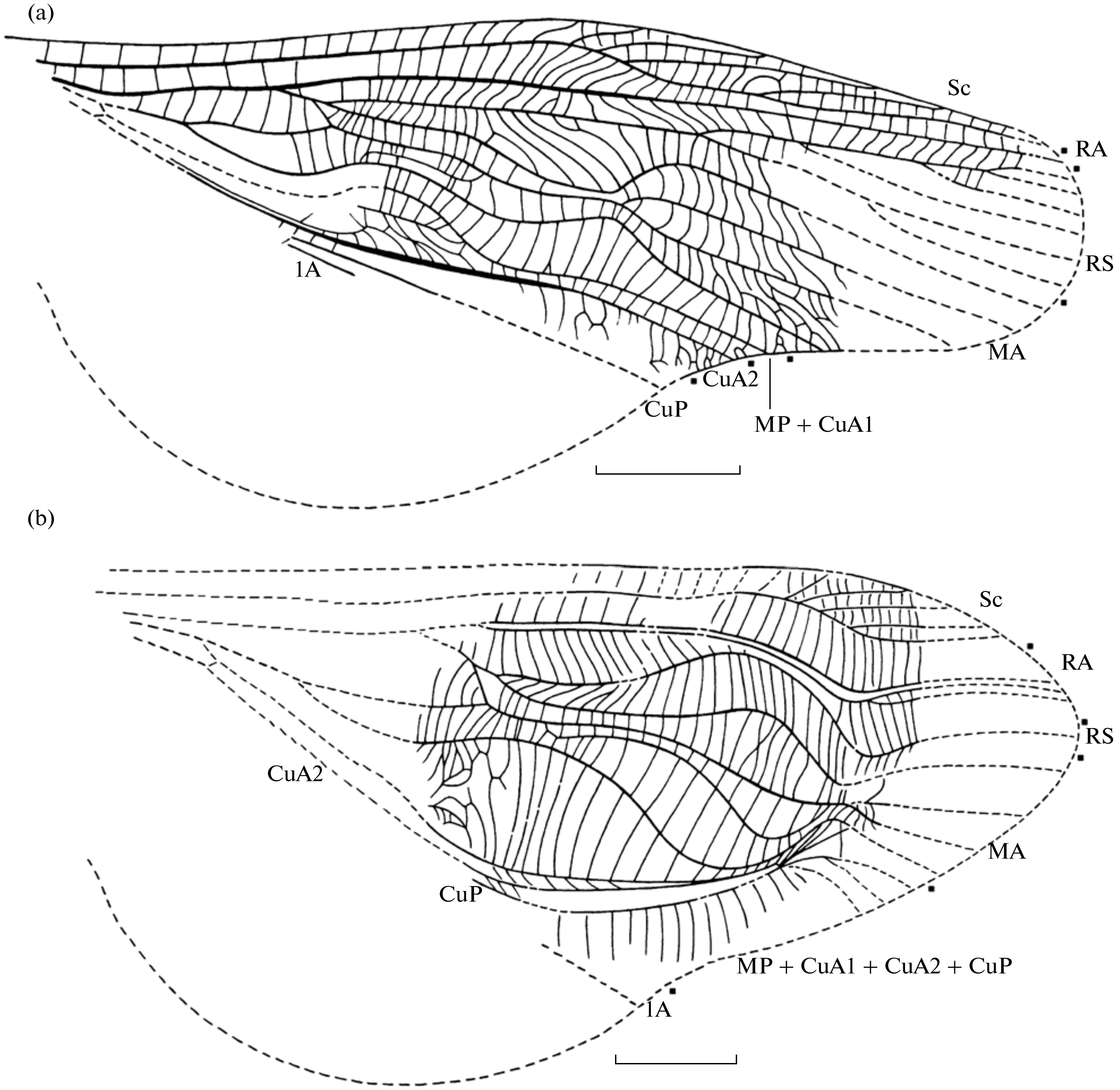


Fig. 87. Impressions, possibly, of male hindwings of a member of Deinotitanidae, without apex, proximal area, and anal fan: (a) *Monstrotitan monstrosus* gen. et sp. nov., holotype PIN, no. 3840/504, Isady locality, Vologda Region; Severodvinian Stage; (b) *Deinotitan orenburgensis* Gor., holotype PIN, no. 3700/167, new interpretation of venation in the holotype (after Gorochov, 2007b, modified), Novo-Aleksandrovka locality, Orenburg Region; Severodvinian Stage.

in Fig. 87b) and *Monstrotitan* gen. nov. (Figs. 86a–86c; 87a).

Comparison. The Deinotitanidae differ from all other families of the order in the presumable presence of a well-developed stridulatory apparatus in the hindwings in combination with the absence of this structure in the forewings.

Remarks. This family was originally described as a subfamily of the family Mesotitanidae, order Titanoptera (Gorochov, 2007b). To date, it has only been known from a single wing fragment from the Upper Permian, with a large stridulatory apparatus similar to that of Mesotitanidae (*Deinotitan orenburgensis* Gor.). This apparatus was initially interpreted as belonging to the forewing and homologous to the stridulatory apparatus of Triassic titanopterans, but the approximately contemporaneous new records described below cast doubt on this interpretation. These specimens are relatively abundant impressions of wing fragments, which fall into two groups.

One group probably comprises forewing fragments, since the anal fan in them is definitely absent. Judging from these fragments, these wings lacked a clear stridulatory apparatus and resemble in venation the forewings of orthopterans of the superfamily Oedischioidea (Figs. 86a, 86b). The second group comprises fragments with significantly narrower costal area, without crossveins between the branches of Sc, and with a stridulatory apparatus similar in structure to that of the genus *Deinotitan* Gor. The most complete of these fragments seem to have a somewhat dilated anal lobe, which is folded fanlike along 1A and tucked under the remaining part of the wing, although traces of this lobe are very weak and hardly discernible (Figs. 86c, 87a).

Both groups of fragments share a number of features: subequal size of many visible structures, which suggests approximately the same wing size; S-shaped curve in the stem of Sc in its distal half; long, closely set, and almost longitudinal distal branches of SC; and somewhat dilated part of the Sc–RA area (near the above-mentioned curve of the stem of Sc) provided with very dense crossveins and darkened (denser?) membranes between them (Figs. 1a, 1c, 2a). The last structure resembles the pterostigma of some cockroaches (Gorochov, 2007a, text-figs. 3a–3c; 4a–4d) and Elcanoidea (Gorochov et al., 2006, text-figs. 2–8); it is more or less developed in the forewings and hindwings of some Triassic titanopterans (Sharov, 1968, text-figs. 48c, 48d, 49b; Gorochov, 2003, text-figs. 1b, 1c, 3a), but unknown in Oedischioidea.

Thus, the above-mentioned fragments possibly belong to members of the order Titanoptera that still did not have a stridulatory apparatus in the forewings, but independently acquired a special stridulatory apparatus in the hindwings. This interpretation is supported by the similarity with Titanoptera in the presence of a pterostigma in both pairs of wings and in the weakly dilated costal area with crossveins between branches of Sc in the forewing (by the way, this type of the costal area has also been recorded in the genus *Permotitan* Gor. from the Middle Permian, the assignment of which to Titanoptera is also questionable: Gorochov, 2004, text-fig. 8e).

However, it is not improbable that Deinotitanidae belonged to orthopterans related to Oedischioidea, although the presence of a pterostigma, partial reduction of branches of MP + CuA1 in the forewing, and weak parallelization of forewing venation in Deinotitanidae contradicts a close position of Deinotitanidae to any family of Oedischioidea. In any case (whether or not the Deinotitanidae belong to Titanoptera or Orthoptera), the group in question should currently be interpreted as a separate family; however, it should be noted that the presence in the hindwing of a stridulatory apparatus alone is not a doubtless basis for the establishment of a new family-group taxon [such an apparatus has independently been developed in the hindwing of some acridoids of the subfamily Pyrgomorphinae, extant katydids of the subfamily Pseudophyllinae (Gorochov and Volchenkova, 2001), and the phasmid genus *Haaniella* Kirby (Gorochov, 2001)].

The above assumptions require confirmation based on better preserved specimens; therefore, only a provisional (very brief) new diagnosis is proposed here for Deinotitanidae (see above).

Genus *Monstrotitan* Gorochov, gen. nov.

Etymology. From the Latin *monstrosus* (monstrous) and the generic name *Deinotitan*.

Type species. *M. monstrosus* sp. nov.

Diagnosis (Figs. 86c, 87a, 90a). Wing (probably hindwing). Costal area in proximal half somewhat narrower than adjacent part of subcostal area and provided only with short and almost vertical branches, without crossveins between them; in distal half, costal area slightly dilated and filled with long and almost longitudinal branches of Sc, with many crossveins between them. Subcostal area with dilated part (probably pterostigma) in distal half, provided with more oblique, more S-shaped, and more densely spaced crossveins than in other parts of this area. RA single; RS with base located in proximal half of wing and with more than two branches; vein looking like most proximal branch of RS (but actually probably being anterior branch of MA) diverging not far from base of RS and rather far from other branches of RS; this vein curved, forming dilated space between it and stem of RS. Short proximal part of anterior branch of MA (up to its anastomosis with RS) probably present, but positioned unusually: its base shifted distal to its apex; middle branch of MA deeply bifurcating in distal part; base of posterior branch of MA located somewhat proximal to base of RS. MP + CuA1 single, with rather short arcuate curvature in middle part; CuA2 also single, but straighter than MP + CuA1.

Species composition. Type species.

Comparison. The new genus differs from the genus *Deinotitan* in the following features: single RA; greater number of branches of RS; less curved stem of RS; less dilated area between RS and the anterior branch of MA; MP + CuA1, CuA2, and CuP not fused together distally; and narrowed (rather than sharply dilated) part of the area between the posterior branch of MA and MP + CuA1, located not far from the bases of the anterior and middle branches of MA (the characters listed, except the first two, only allow the identification of hindwings and only from those forms of the genus *Deinotitan* that had a well-developed stridulatory apparatus in the hindwing).

Remarks. Specimens PIN, nos. 3840/655 and 660, collected in the same locality as the holotype of type species and possibly representing forewings of *Monstrotitan* (Figs. 86a, 86b), are also tentatively assigned to this genus. However, since this assumption is not sufficiently reliable, the characters of these wings are not included in the diagnosis of the new genus.

Monstrotitan monstrosus Gorochov, sp. nov.

Etymology. The Latin *monstrosus* (monstrous).

Holotype. PIN, no. 3840/504, part and counterpart, possibly male hindwing without proximal part, anal fan, and apex; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 87a, 90a). The S-shaped curvature of Sc is located not far from the middle of the wing; the distal branches of this vein are very long; the area between RS and RA is not dilated; the base of RS is located markedly proximal to the middle of the wing; the anterior branch of MA is rather strongly and almost angularly curved in middle part; a short additional (secondary) longitudinal vein is present between the middle and posterior branches of MA; the posterior branch of MA and the single MP + CuA1 are strongly sinuate; each of the two areas between CuA2 and the posterior branch of MA has a markedly dilated part; the middle part of CuA2 is strongly thickened (it is probably the rubbing part of the stridulatory apparatus). The coloration of the wing is apparently transparent, but with a darkened region of densely spaced crossveins between Sc and RA (pterostigma).

Measurements, mm. Length of impression, 37; estimated wing length, 40–42.

Remarks. Note that the venation of the presumable hindwings (specimens PIN, nos. 3840/1217 and 1224) with an underdeveloped stridulatory apparatus (Fig. 86c) considerably differs from that of the holotype and paratypes in the following characters: the S-shaped curvature of Sc is positioned clearly closer to the wing apex; the distal branches of this vein are generally shorter; the base of RS is located only slightly proximal to the middle of the wing; the anterior branch of MA is curved markedly weaker; the additional (secondary) longitudinal vein between the middle and posterior branches of MA is undeveloped; the posterior branch of MA and the single MP + CuA1 are clearly less sinuate; each of two areas between CuA2 and the posterior branch of MA has a weakly dilated part; the middle part of CuA2 is not thickened. These differences can be interpreted as either differences between species or sexual dimorphism (e.g., male could have a normally developed stridulatory apparatus, but, in female, it could have been underdeveloped and nonfunctional, developed as a result of carry-over of male characters on females). The forewing venation (Figs. 86a, 86b) differs from that of presumable hindwings even more strongly: in the total absence of a stridulatory apparatus (namely, dilated sound-producing areas); in the position of the bases of a number of veins closer to the wing base; in the presence of a three-branched (instead of a single) MP + CuA1; in the position of the pterostigma, located closer to the wing apex than even in the presumable female hindwings. Therefore, it is not completely clear that these wings and presumable hindwings belong to the same species, genus, and even the same higher-rank taxon. In addition, sex identification in particular forewing fragments remains unreliable and it is even uncertain whether or not they belong to the same species (Figs. 86a and 86b show forewings slightly differing in the width of the subcostal area near the base of RS and in the position of the apex of the middle branch of MP + CuA1).

Material. Holotype and paratypes: PIN, nos. 3840/503, 1218, 1222, and 1225 from the same locality as the holotype; PIN, no. 5103/289 from the Balymotikha locality (Vladimir Region; Upper Permian, Vyatkian Stage). All paratypes are fragments, possibly of the male hindwing, less complete than the holotype. The following impressions are tentatively attributed to this species: specimens PIN, nos. 3840/1217, 1224, fragments of two wings, possibly hindwings, with an underdeveloped stridulatory apparatus from the same locality as the holotype; specimens PIN, nos. 3840/416, 655, 660, 661, 665, 678, 1209, 1210, 1214, 1215, 1216, 1219, 1220, 1221 and 1223, various fragments of forewings or presumably forewings from the same locality.

Order Orthoptera Olivier, 1789

Suborder Ensifera Chopard, 1920

Infraorder Elcanidea Handlirsch, 1906

Superfamily Elcanoidea Handlirsch, 1906

Family Permelcanidae Sharov, 1962

Subfamily Meselcaninae Gorochov, 1989

This subfamily was established for a single Triassic genus, *Meselcana* Shar. (Gorochov, 1989). It was later shown that the Meselcaninae also occurred in the Permian (Gorochov, 2007b), but the description of that material is provided only now. Surprisingly, even Middle Permian members of this subfamily are close to Triassic taxa in their forewing morphology, so that they are included in the same genus. However, wings of Permian Elcanoidea were probably already strongly specialized for four-wing flight; therefore, their morphology was probably very functional and more strongly stabilized than that of many other structures. Therefore, it seems plausible that, as fossil bodies of Meselcaninae are found, the generic assignment of Permian species of this subfamily will be reviewed.

Genus *Meselcana* Sharov, 1968

Meselcana udmurtica Gorochov, sp. nov.

Etymology. From Udmurtia.

Holotype. PIN, no. 3286/12, part and counterpart of forewing without proximal portion; Chepanikha locality, Udmurtia; Urzhumian Stage.

Description (Figs. 88a, 90b). Forewing. The apex of the costal area almost reaches the middle of the interradial area; the latter area is significantly dilated in the proximal half because of an arcuate curvature in the stem of RA; the distance between the apices of Sc and RA is subequal to that between the apex of Sc and base of RS; RS and MA together have six long branches; MP + CuA1 is three-branched; the proximal part of CuA1 (to its anastomosis with MP) is long, more than thrice as long as the proximal part of MP. Coloration is only preserved in the distal part of the wing, which is almost entirely darkened, but has lighter (semitransparent?) central part of membrane in some cells.

Measurements, mm. Length of impression, 17.5; estimated wing length, 20.

Comparison. The forewing of the new species differs from that of Triassic species of the genus (*M. madygenica* Shar. and *M. permelcanoides* Gor.) in the shorter Sc (yet far not as short as in Permelcaninae Shar.) and in the more dilated proximal half of the interradial area; additionally, the new species differs from *M. permelcanoides* in the primitive position of the posterior branch of MA (which is not shifted on MP + CuA1).

Material. Holotype. The following impressions possibly also belong to this species: specimens PIN, nos. 3286/34, 36, and 81, fragments of three forewings from the same locality as the holotype. These fragments are similar to the holotype, but have the proximal part of CuA1 somewhat shorter than in the holotype; a number of other structures mentioned in the description and coloration are insufficiently preserved.

Meselcana vologodica **Gorochov, sp. nov.**

Etymology. From the Vologda Region.

Holotype. PIN, no. 3840/654, part and counterpart of almost complete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 88b, 90c). The forewing is similar in morphology to that of *M. udmurtica,* but the apex of the costal area is positioned clearly distal to the middle of the interradial area; the distance between the apices of Sc and RA is significantly smaller than the distance between the apex of Sc and the base of RS; RS and MA together have seven long branches; the proximal part of CuA1 (to its anastomosis with MP) is short, less than twice as long as the proximal part of MP. The coloration of the wing is light (transparent?), but with darkened longitudinal veins, membranes in the region of free branches of RA (pterostigma), and narrow stripes along both sides of the crossveins between branches of RS.

Measurements, mm. Wing length, 18.

Comparison. The forewing of the new species differs from that of both Triassic species of the genus in the more dilated proximal half of the interradial space; it also differs from *M. madygenica* in the clearly shorter proximal part of CuA1 and from *M. permelcanoides* in the primitive position of the posterior branch of MA (which is not shifted on MP + CuA1). The differences of the new species from *M. udmurtica* are listed above (in the description of *M. vologodica*).

Material. Holotype. The following impressions of fragments of two other forewings probably also belong to this species: specimen PIN, no. 3840/1211 from the same locality as the holotype; specimen PIN, no. 3700/168 from the Novo-Aleksandrovka locality (Orenburg Region; Upper Permian, Severodvinian Stage). Both fragments are similar to the holotype, but insufficient for more precise identification; for example, in the specimen from Isady, the proximal part of CuA1 is somewhat longer than in the holotype and in the specimen from Novo-Aleksandrovka, but still shorter than in the specimens of *Meselcana udmurtica* from Chepanikha.

Infraorder Oedischiidea Handlirsch, 1906

Superfamily Oedischioidea Handlirsch, 1906

Family Oedischiidae Handlirsch, 1906

Subfamily Tcholmanvissiinae G. Zalessky, 1934

Tcholmanvissiinae incertae sedis

Material. The following impressions have been attributed to this subfamily: specimens PIN, nos. 3286/82, 83, and 84, small fragments of large wings (presumably hindwings); Chepanikha locality (Udmurtia; Urzhumian Stage). More precise identification of such an insufficient material is impossible.

Family Pruvostitidae M. Zalessky, 1929

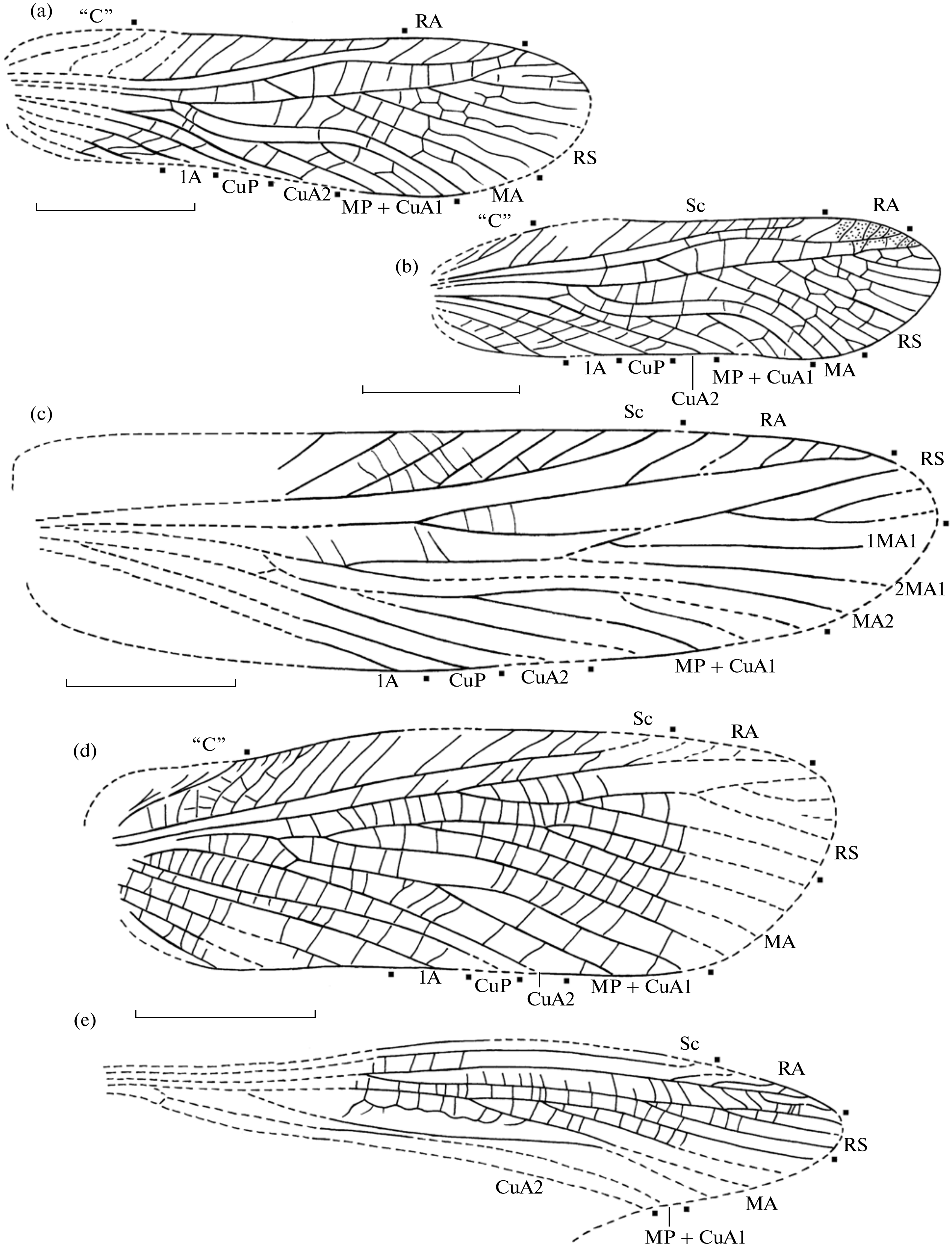
?Subfamily Pruvostitinae M. Zalessky, 1929

The family Pruvostitidae is only known from the Permian (Gorochov, 1987a, 1995). The subfamily Pruvostitinae differs from other subfamilies of the family only in the primitive characters of the forewing: the presence of contact between RS and the first branch of MA (1MA1) or fusion of short parts of these veins with each other (from Tettavinae Sharov, 1968 and Maculoedischiinae Gorochov, 1987); and the proximal branch of Sc crossed by the distal part of the false costal vein (from Sylvoedischiinae Gorochov, 1987 and Maculoedischiinae). The forewing impression described below certainly belongs to the family Pruvostitidae, as its Sc has more or less long branches and regular crossveins between them; based on the presence of contact between RS and 1MA1, it can be assigned to Pruvostitinae or Sylvoedischiinae. However, more precise identification is difficult, because the proximal portion of the wing is not preserved and the morphology of the false costal vein and the proximal branch of Sc is impossible to determine. Nevertheless, this impression is provisionally included in Pruvostitinae, because of the strong S-shaped curvature in the reconstructed stem MP + CuA1 and longitudinally sloping branches of this vein; these features are not known among Sylvoedischiinae, but occur among Pruvostitinae.

Genus *Suchonoedischia* Gorochov, gen. nov.

Etymology. From the Sukhona River and the generic name *Oedischia.*

Type species. *S. incompleta* sp. nov.


(a)
"C"
RA
RS
1A
CuP
CuA2
MP + CuA1
MA
Sc
RA
"C"
(b)
RS
1A
CuP
MP + CuA1
MA
CuA2
(c)
Sc
RA
RS
1MA1
2MA1
MA2
1A
CuP
CuA2
MP + CuA1
Sc
RA
"C"
(d)
RS
MA
1A
CuP
CuA2
MP + CuA1
(e)
Sc
RA
RS
CuA2
MA
MP + CuA1

Diagnosis (Figs. 88c, 90d). Forewing. Sc with relatively sparse branches and with apex located rather far from wing apex (approximately as far as place of contact between RS and 1MA1); subcostal area not dilated proximal to base of RA. Stem of RA almost straight, with relatively numerous, almost straight, and rather short branches, forming regular and relatively sparse comb (space occupied by these branches long and narrow); RS with long proximal part (before its contact with 1MA1), only slightly shorter than remaining part of RS stem and with only a few branches; interradial area rather narrow. Space between proximal part of MA1 (before its division into 1MA1 and 2MA1) and MA2 narrow; stem MP + CuA1 strongly S-shaped; its branches not numerous and gently sloping (almost longitudinal).

Species composition. Type species.

Comparison. The new genus resembles *Sharovoedischia* Gorochov, 1987 (from the Lower Permian of the Perm Region) *Pruvostites* M. Zalessky, 1929, and *Kitjakoedischia* Gorochov, 1987 (from the Middle Permian of Tatarstan and Kirov Region, respectively) in the long proximal part of RS (before its contact with 1MA1), the significant S-shaped curvature of the stem of MP + CuA1, and the gently sloping branches of this stem. However, it is distinguished from these genera by the following characters: from *Sharovoedischia,* by the straight stem of RA with almost straight branches (forming a narrow, long, sparse, and regular comb) and the fewer branches of RS; from *Pruvostites,* by the sparse branches of Sc and the narrow area of MA1–MA2; from *Kitjakoedischia,* by the subcostal area not dilated proximal to the base of RS and the fewer branches of MP + CuA1.

Suchonoedischia imcompleta Gorochov, sp. nov.

Etymology. The Latin *incompleta* (incomplete).

Holotype. PIN, no. 3840/663, negative impression of distorted forewing without proximal one-third and apex; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 88c, 90d). RA has six branches; the base of the proximal one is located slightly proximal to the apex of Sc. RS has three branches, which occupy a very small area in the distal wing part. The base of the distal (longer) part of 1MA1 is shifted towards the wing base up to the middle of the short proximal part of this vein, positioned between the point of division of MA1 and the place of contact between 1MA1 and RS (so that the distal part of 1MA1 looks diverging from the middle of the proximal part of 1MA1). MP + CuA1 has three preserved branches (but probably had four). The proximal parts of CuA2, CuP, and 1A are sloping rather gently (almost longitudinal); the apex of CuP is positioned slightly distal to the point of bifurcation of R. Coloration is not preserved.

Measurements, mm. Length of impression, 19; estimated wing length, 27–29.

Material. Holotype.

Family Proparagryllacrididae Riek, 1956

Subfamily Kashgarlimahmutiinae Koçak et Kemal, 2008 (May)

Ferganiinae: Gorochov, 1987.
Ademirsoyinae: Özdikmen, 2008 (June).

This subfamily was originally described as Ferganiinae (Gorochov, 1987b) to comprise two Triassic genera: *Kashgarlimahmutia* Koçak et Kemal, 2008 (=*Fergania* Sharov, 1968 =*Ademirsoyus* Özdikmen, 2008) and *Parafergania* Gorochov, 1987. The name of the subfamily was based on *Fergania,* a genus of Triassic orthopterans twice renamed by Turkish colleagues because of the homonymy of its name (Gorochov and Maehr, 2008). A new genus of this subfamily is described below; thus, the family is recorded in the Paleozoic for the first time; this record is simultaneously the first record of the family Proparagryllacrididae in the Paleozoic.

Genus *Archifergania* Gorochov, gen. nov.

Etymology. From the latinized Greek *archi* (beginning) and *Fergania,* formerly used as orthopteran generic name.

Type species. *A. isadyensis* sp. nov.

Diagnosis (Figs. 88d; 90e). Forewing. Sc long (more than twice as long as wing wide), with rather dense proximal branches. Interradial area in region of division of RS not dilated. MA starting branching markedly proximal to base of RS, with at least four more or less long branches; proximal part of MP (before its anastomosis with CuA1) well developed, not resembling crossvein. MP + CuA1 two-branched; apex of its posterior branch located markedly distal to base of RS. Space between CuA2 and anal margin of wing clearly longer than space between branches of MP + CuA1.

Species composition. Type species.

Comparison. The new genus differs from both Triassic genera of the family in the forewings with more densely spaced proximal branches of Sc, greater

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Fig. 88. Members of (a, b) Permelcanidae, (c) Pruvostitidae, and (d, e) Proparagryllacrididae: (a) *Meselcana udmurtica* sp. nov., holotype PIN, no. 3286/12, forewing without proximal portion, Chepanikha locality, Udmurtia; Urzhumian Stage; (b) *M. vologodica* sp. nov., holotype PIN, no. 3840/654, almost complete forewing; (c) *Suchonoedischia incompleta* gen. et sp. nov., holotype PIN, no. 3840/663, unfolded forewing fragment without proximal half; (d) *Archifergania isadyensis* gen. et sp. nov., holotype PIN, no. 3840/1190, forewing without part of precostal field and distal portion; (e) specimen PIN, no. 3840/319, hindwing fragment possibly belonging to *A. isadyensis*; Isady locality, Vologda Region; Severodvinian Stage.

distance between the proximal bifurcations of R and MA2, and the proximal part of MP not resembling a crossvein (primitive condition); additionally, it differs from the type genus in the fewer branches of MP + CuA1 in the forewing (advanced condition).

Archifergania isadyensis Gorochov, sp. nov.

Etymology. From the Isady locality.

Holotype. PIN, no. 3840/1190, part and counterpart of forewing without distal portion and base of precostal area; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 88d; 90e). Sc has at least ten more or less long branches; RS has at least two long branches; the proximal bifurcation of MA is located not far from the base of MP; the proximal part of the space between CuA2 and CuP is somewhat dilated. The preserved part of the wing is darkened, but has a broad nondarkened (possibly, dark coloration is merely not preserved in some areas) band along its costal margin (this band includes the entire costal area and all areas between the distal half of Sc and posterior branches of MA), a rather small region near the distal parts of CuP, 1A, and 2A, and small spots in the middle of cells in the darkened part of the wing between CuP and the proximal half of Sc.

Measurements, mm. Length of impression, 16; estimated wing length, 20.

Material. In addition to the holotype, specimen PIN, no. 3840/319, an impression of a small fragment, possibly of the hindwing, from the same locality as the holotype is provisionally attributed to this species. This fragment has a three-branched RS and a four-branched MA; in addition, the area between the first (proximal) and second branches of MA is dilated and provided with a thin sinuate secondary longitudinal vein (Fig. 88e).

Order Phasmatoptera Beier, 1955

Superfamily Prochresmodoidea Vishniakova, 1980

?Family Permophasmatidae Gorochov, 1992

To date, the family has been known from one small wing fragment from the Upper Permian of Mongolia (Gorochov, 1992, 1994). It is readily distinguished from the Triassic genera *Prochresmoda* Sharov, 1968 and *Triassophasma* Gorochov, 1994 of the family Prochresmodidae Vishniakova, 1980 by the tegmina with a branching RS, the base of which is located distal to the point of the division of MA, and with the area between CuA2 and CuP wider in the region of the base of MA than the nearest part of the area between M and CuA2. The nomenclature of veins used here follows Sharov (1968), although the homology proposed by him for some veins of phasmids and orthopterans requires a revision, which is presently impossible because of the absence of any data on wing morphology of Phasmatoptera earlier than the Late Permian and because all known later phasmids have a partially reduced venation.

The recently found new forms from the Triassic and Permian look more or less intermediate between the above-discussed taxa: the elytron of the Triassic genus *Palaeochresmoda* Nel et al, 2004 has a one-branched RS and a narrow area of CuA2–CuP (as in *Prochresmoda* and *Triassophasma*), but the base of its RS is located distal to the point of bifurcation of MA (as in Permophasmatidae); the Permian tegmina described below are characterized by two-branched RS (as in Permophasmatidae), the position of the base of RS proximal to the point of division of MA, and a narrow CuA2–CuP area (as in Prochresmoda and Triassophasma). Thus, at present, all these forms are tentatively assigned to the above-mentioned families; the genus *Palaeochresmoda* is provisionally included here in the family Prochresmodidae (because its similarity to Permophasmatidae in the position of the base of RS in relation to the point of division of MA could have developed in parallel), and the new Permian phasmids are assigned to the primitive paraphyletic family Permophasmatidae based on the presence of at least two branches of RS (symplesiomorphy).

Note that, in a recent paper on Triassic phasmids (Nel et al., 2004), the presence of a sinuate intercalary vein between RA and RS in Permophasmatidae was interpreted as a possibly unique character among pre-Cenozoic phasmids. This statement is perplexing, because a similar additional longitudinal vein is present in the elytra of *Triassophasma brevipoda* (Sharov, 1968) and *T. intermedium* Gorochov, 1994 (Gorochov, 1994, text-figs. 3i, 3k), and rudiments of this vein are visible in the elytra of *T. pusillum* Gorochov, 1994, *T. minutissimum* Gorochov, 1994, *Prochresmoda media* Gorochov, 1994, and *Palaeochresmoda grauvogeli* Nel et al., 2004 (this vein is also present in the majority of Permian specimens described below).

Genus *Isadyphasma* Gorochov, gen. nov.

Etymology. From the Isady locality and the generic name *Phasma*.

Type species. *I. bashkuevi* sp. nov.

Diagnosis (Figs. 89a–89e, 90f–90h). Forewing. Sc and false C long; false C extending beyond point of bifurcation of MA, or reaching or almost reaching this point; Sc reaching apical wing part. RA one-branched; RS two-branched, with base located in middle part of wing. MA two-branched, but sometimes one of its branches partially reduced or with several short additional branches; point of bifurcation of MA located distal to base of RS. MP + CuA1 single, distinctly convex. CuA2 and CuP, as in Prochresmodidae, diverging from each other in proximal part of tegmen, but not at its very base; area between CuA2 and CuP near base of MP + CuA1 narrower than nearest part of area between MP + CuA1 and CuA2. Only first branch of 2A normally developed; its other

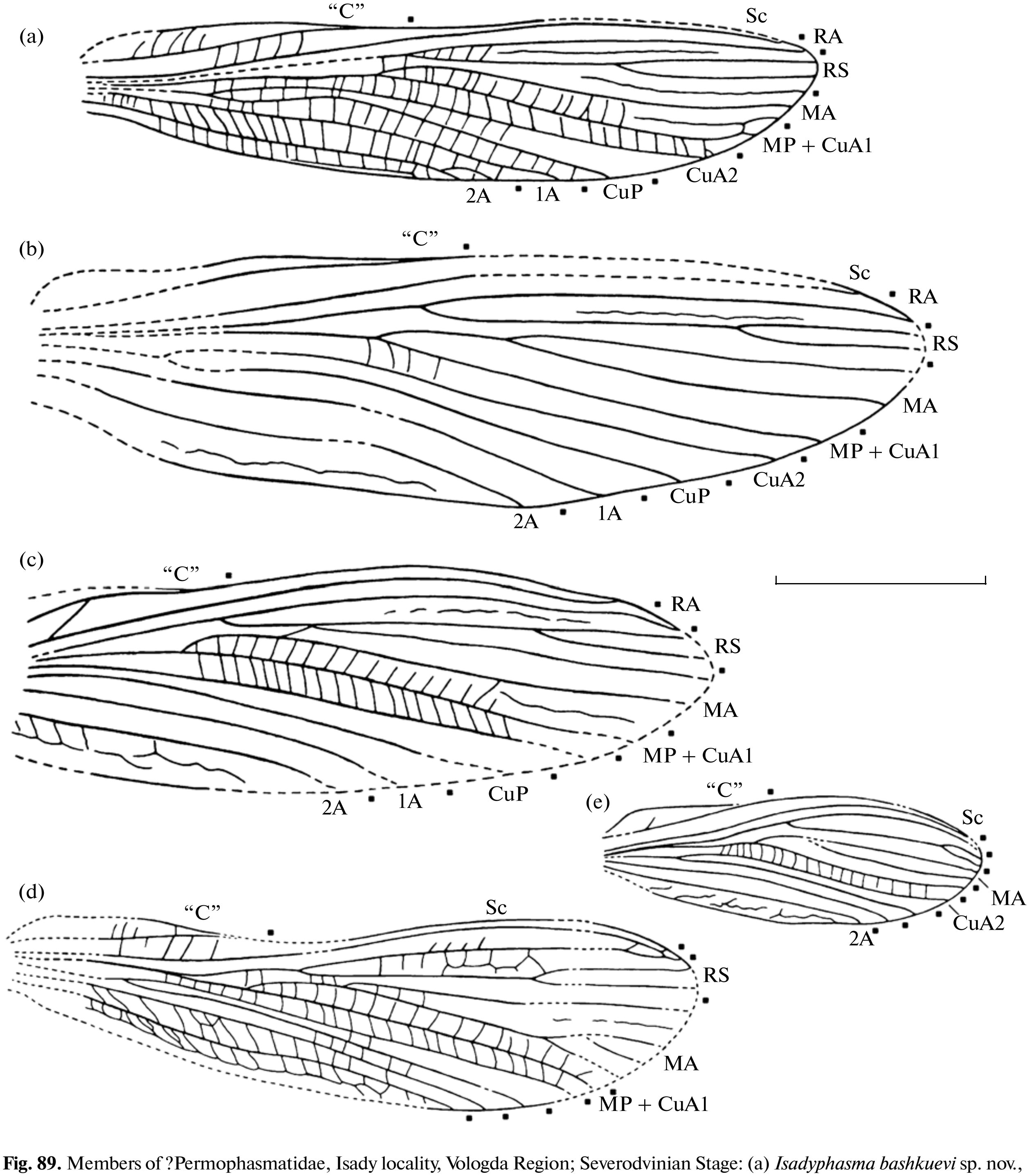

Fig. 89. Members of ?Permophasmatidae, Isady locality, Vologda Region; Severodvinian Stage: (a) *Isadyphasma bashkuevi* sp. nov., holotype PIN, no. 3840/507, forewing, possibly male; (b) *I. ?bashkuevi* sp. nov., specimen PIN, no. 3840/505, forewing, possibly female, without proximal area; (c) *I. ? bashkuevi* sp. nov., specimen PIN, no. 3840/1227, forewing fragment, possibly female; (d) *I. suchonae* sp. nov., holotype PIN, no. 3840/1228, forewing without proximal area; (e) *I. deminutum* sp. nov., holotype PIN, no. 3840/1231, forewing.

branches reduced (only represented by traces in shape of one sinuate longitudinal veinlet, sometimes interrupted and/or not very distinct).

Species composition. In addition to the type species, *I. suchonae* sp. nov. and *I. deminutum* sp. nov.

Comparison. The tegmina of the new genus differs from that of *Permophasma* in the following characters: the base of MP + CuA1 and points of bifurcation of RS and MA are more distal; the area between MP + CuA1 and CuA2 near the base of MP + CuA1 is wider than the nearest part of the CuA2–CuP

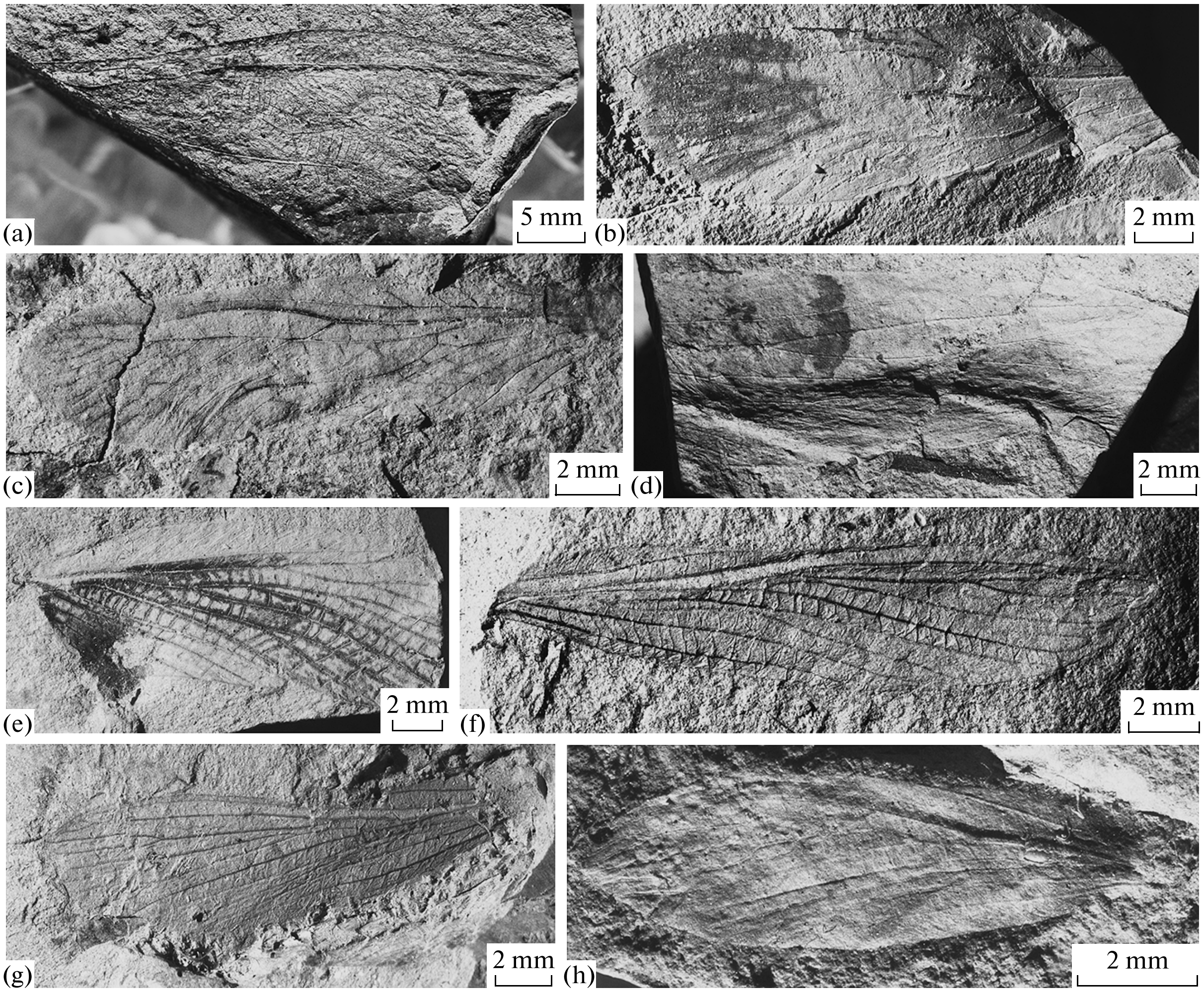

Fig. 90. Orthopteroid insects from the Permian of European Russia: (a) *Monstrotitan monstrosus* gen. et sp. nov., holotype PIN, no. 3840/504; Isady locality, Vologda Region; Severodvinian Stage; (b) *Meselcana udmurtica* sp. nov., holotype PIN, no. 3286/12, forewing without proximal portion, Chepanikha locality, Udmurtia; Urzhumian Stage; (c) *M. vologodica* sp. nov., holotype PIN, no. 3840/654, almost complete forewing; (d) *Suchonoedischia incompleta* gen. et sp. nov., holotype PIN, no. 3840/663, unfolded forewing fragment without proximal part; (e) *Archifergania isadyensis* gen. et sp. nov., holotype PIN, no. 3840/1190, forewing without area of precostal field and distal portion; (f) *Isadyphasma bashkuevi* sp. nov., holotype PIN, no. 3840/507, forewing, possibly male; (g) *I. suchonae* sp. nov., holotype PIN, no. 3840/1228, forewing without proximal area; (h) *I. deminutum* sp. nov., holotype PIN, no. 3840/1231, forewing; Isady locality, Vologda Region; Severodvinian Stage.

area; the additional (secondary) longitudinal vein between 1A and 2A is undeveloped.

Isadyphasma bashkuevi Gorochov, sp. nov.

Etymology. In honor of one of collectors, the paleoentomologist A. Bashkuev.

Holotype. PIN, no. 3840/507, part and counterpart of almost complete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 89a, 90f). RS bifurcates somewhat distal to the middle of the interradial area, which is provided with a distinct longitudinal veinlet. MA is single, but between it and RS, there is a sinuate longitudinal vein, which is practically not connected with M and looks like an additional veinlet (but possibly represents a rudimentary anterior branch of MA); MP + CuA1 is also single, and there is a short additional longitudinal vein between it and MA. The area between CuA2 and CuP in the region near the base of MP + CuA1 is half (or slightly less) as wide as the nearest parts of both M–CuA2 and CuP–1A areas. The distance between the base of MA and the apex of 2A is less than half the distance between the apex of 2A and wing apex. Coloration is not preserved.

Measurements, mm. Length of impression, 18; estimated wing length, 19.

Material. Holotype. Several impressions from the same locality have also been attributed to this species: specimen PIN, no. 3840/505, fragment of a large forewing without proximal portion (impression is 21 mm long; estimated wing length 23–24 mm), with clearly two-branched MA and the CuA2–CuP area somewhat less narrowed than in the holotype (Fig. 89b); specimen PIN, no. 3840/1227, forewing fragment, similar to the previous one, but with the anterior branch of MA connected to RS near the base of this MA branch (Fig. 89c); specimen PIN, no. 3840/1229, fragment of a rather small forewing, similar in size to the holotype, but with insufficiently distinct venation. The provisional attribution of these impressions to the new species is based on the assumptions that the larger wings probably belong to females and, in the smaller males, the first branch of MA was probably more strongly reduced (in female, only early stages of this process are possible, but in male, this branch can turn into a sinuate veinlet that has practically lost its connection with M and looks like an additional intercalary vein).

Isadyphasma suchonae Gorochov, sp. nov.

Etymology. From the Sukhona River.

Holotype. PIN, no. 3840/1228, positive impression of slightly distorted forewing without proximal part; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 89d, 90g). The wing is similar to that of *I. bashkuevi,* but its apical portion is somewhat wider because of the development of two short additional branches in the distal part of the second branch of MA; an additional longitudinal veinlet is present in the area between the first and second branches of MA; such a vein is absent in the area between MA and MP + CuA1; the distance between the base of MA and the apex of 2A is subequal to the distance between the apex of 2A and wing apex. Coloration is not preserved.

Measurements, mm. Length of impression, 15.5; estimated wing length, 17–18.

Comparison. The differences between the new species and *I. bashkuevi* are listed above (in the description of *I. suchonae*).

Material. Holotype.

Isadyphasma deminutum Gorochov, sp. nov.

Etymology. Neutral form of the Latin *deminutus* (diminished).

Holotype. PIN, no. 3840/1231, part and counterpart of almost complete forewing; Isady locality, Vologda Region; Severodvinian Stage.

Description (Figs. 89e, 90h). The wing is similar to that of *I. bashkuevi,* but distinctly smaller and somewhat shorter (almost oval in shape); RS bifurcates markedly distal to the middle of the interradial area; MA has two branches; all areas between RA and MP + CuA1 lack visible additional longitudinal veinlets; the CuA2–CuP area is not distinctly narrowed in the region of the base of MA; the distance between the base of MA and the apex of 2A is subequal to the distance between the apex of 2A and wing apex. Coloration is partially preserved; the entire wing was probably uniformly darkened.

Measurements, mm. Wing length, 9.5.

Comparison. The new species differs from *I. suchonae* in the following characters: the forewing is markedly smaller and shorter; the point of bifurcation of RS is distinctly closer to the wing apex; the second branch of MA is single; additional longitudinal veinlets in the interradial area and between branches of MA are undeveloped. The differences of the new species from *I. bashkuevi* are listed in the description. Since all longitudinal veins of the wing of the new species are well pronounced (approximately to the same extent as in congeners), the wing was apparently not nymphal, i.e., *I. deminutum* was probably just a short-winged species (like many modern phasmids).

Material. Holotype.

3. RESULTS AND DISCUSSION

3.1. Insects of the Permian and Early Triassic (Urzhumian–Olenekian Ages) and the Problem of the Permian–Triassic Biodiversity Crisis

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The extensive material of fossil insects from Biarmian and Tatarian localities of European Russia, collected mostly by expeditions of the Arthropoda Laboratory, PIN, during the last decade and described in the previous chapters of this volume, once again raise the question of the character of changes in the composition of the largest group of living organisms at the most dramatic boundary in the Phanerozoic history of life: at the Permian–Triassic boundary and around it. This question is the subject of this chapter.

3.1.1. Materials

The data on the Urzhumian–Induan fossil insect localities of European Russia are given above (Chapter 1). Brief data on other materials from localities of this age outside European Russia are added below.

Suriekova 1. Russia, Kemerovo Region, Kuznetskii District, left bank of the Tom River upstream from the mouth of the Suriekova River; Middle Permian, Urzhumian Stage, Kol'chugino Group, Il'inskoe Subgroup, Kazankova–Markina Formation (Shcherbakov, 2008);

judging from the insect assemblage, Severodvinian Stage (see below). A total of 670 insect specimens have been collected; they are stored in PIN (Rohdendorf et al., 1961).

Order Tripida. Family Lophioneuridae (Vishniakova, 1981).

Order Hemiptera. Families Archescitinidae (D.E. Shcherbakov, pers. comm.), Prosbolidae, Protopsyllidiidae, Scytinopteridae, Serpentivenidae, and Surijokocixiidae (Shcherbakov, 2000).

Order Paleomanteida. Family Paleomanteidae (Rohdendorf et al., 1961),

Order Coleoptera. Families Permocupedidae, Rhombocoleidae, Schizocoleidae, and Taldycupedidae (Ponomarenko, 2004)

Order Jurinida. Family Jurinidae (see Chapter 2.1).

Order Panorpida. Families Kaltanidae (Rohdendorf et al., 1961)]; Permochoristidae, and Permotipulidae (Novokshonov, 1997).

Order Grylloblattida. Families Liomopteridae and Megakhosaridae (Aristov, 2009b),

Sokolova 2. Russia, Kemerovo Region, Prokop'evskii District, left bank of the Bol'shaya Tykhta River, somewhat upstream from the village of Sokolova; Upper Permian, Severodvinian Stage, Kol'chugino Series, Erunakovo Subseries, Gramoteino Formation (Shcherbakov, 2008). Judging from the insect assemblage, Vyatkian Stage (see below). A total of 569 insect fossils have been collected; stored in PIN (Rohdendorf et al., 1961).

Order Hemiptera. Families Prosbolidae, Scytinopteridae, Dysmorphoptilidae, and Paraknightiidae (Shcherbakov, 2000).

Order Paleomanteida. Family Permosialidae (Rohdendorf et al., 1961).

Order Coleoptera. Families Permocupedidae, Rhombocoleidae, Schizocoleidae, Permosynidae, and Taldycupedidae (Ponomarenko, 2004).

Order Neuroptera. Family Permithonidae (A.G. Ponomarenko, pers. comm.)

Order Jurinida. Family Glosselytridae (see Chapter 2.1)

Order Panorpida. Family Permochoristidae (Novokshonov, 1997).

Karaungir. Kazakhstan, East Kazakhstan Province, Zaisanskii District, Saur Mountain Range, right bank of the Karaungir River 500 m downstream of the mouth of the Maichat Creek (coll. nos. 2494 and 2495); right bank of the Kenderlyk River (coll. no. 2781); Saikan Mountain Range, right bank of the Karaungir River, Kyuryul'tyu gully (coll. no. 3060); Upper Permian, Vyatkian Stage (Shcherbakov, 2008), Maichat and Akkolka Formations. Judging from the insect assemblage, Urzhumian Stage (see below). A total of about 550 specimens have been collected, stored in PIN (*Katalog kollektsii ...,* 2010).

Order Odonata. Family Meganeuridae (identified by D.V. Vassilenko).

Order Tripida. Family Lophioneuridae (Vishniakova, 1981).

Order Hemiptera. Families Archescitinidae, Ingruidae, Pereboriidae, Prosbolidae, Protopsyllidiidae, Dysmorphoptilidae, Scytinopteridae, Serpentivenidae, ?Dunstaniidae, and ?Prosbolopseidae (Shcherbakov, 2000).

Order Paleomanteida. Family Permosialidae (see Chapter 2.1).

Order Coleoptera. Families Permocupedidae, Rhombocoleidae, Schizocoleidae, and Taldycupedidae (Ponomarenko, 2004).

Order Jurinida. Families Jurinidae and Glosselytridae (see Chapter 2.1).

Order Panorpida. Families Kaltanidae and Permochoristidae (Novokshonov, 1997).

Order Trichoptera. Families Protomeropidae (Novokshonov, 1997), Microptysmatidae (see Chapter 2.5).

Order Grylloblattida. Families Liomopteridae, Tshekardominidae, Ideliidae, Megakhosaridae, Blattogryllidae, and Permothermopsidae (Aristov, 2009b)

Order Perlida. Families Palaeonemouridae and Paleoperlidae (Sinitshenkova, 1987).

Bor-Tologoi. Mongolia, South Gobi Province, 16 km southeast of Tsogttsetsii Sum, Bor-Tologoi locality 20 km east-southeast of Tabun-Tologoi quarry; Upper Permian, Severodvinian Stage, Tsankhin Formation. The formation can be correlated with the Leninsk Formation of the Kuznetsk Basin (Shcherbakov, 2008). Based on the insect assemblage, Urzhumian Stage (see below). A total of about 860 specimens have been collected, stored in PIN (*Katalog kollektsii ...,* 2010).

Order Odonata. Family Ditaxineuridae (identified by D.V. Vassilenko).

Order Caloneurida. Family Caloneuridae (Rasnitsyn in Rasnitsyn and Quicke, 2002, p. 108, as Apsidoneuridae).

Order Dictyoneuridae. Family Mongolodictyidae (Sinitshenkova, 1992).

Order Hemiptera. Families Archescitinidae, Boreoscytidae, Prosbolopseidae, Ingruidae, Pereboriidae, Prosbolidae, Scytinopteridae, Dunstaniidae, Stenoviciidae (Shcherbakov, 2000), and Coleoscytidae (*Katalog kollektsii ...,* 2010).

Order Paleomanteida. Families Paleomanteidae (*Katalog kollektsii ...,* 2010) and Permosialidae (Aristov, 2004b).

Order Coleoptera. Families Permocupedidae, Rhombocoleidae, Schizocoleidae, Taldycupedidae, and Asiocoleidae (Ponomarenko, 2004).

Order Corydalida. Family Parasialidae (Ponomarenko, 2000a).

Order Jurinida. Family Glosselytridae (Ponomarenko, 2000a).

Order Neuroptera. Family Permithonidae (*Katalog kollektsii ...,* 2010).

Order Panorpida. Families Kaltanidae (Novokshonov, 1994) and Permochoristidae (Novokshonov, 1997).

Order Trichoptera. Family Microptysmatidae (see Chapter 2.5).

Order Grylloblattida. Families Tshekardominidae, Ideliidae, and Liomopteridae (Aristov, 2009b).

Order Perlida. Family Palaeonemouridae (Dijk and Geertsema, 2004).

Order Forficulida. Family Dermelytridae (*Katalog kollektsii ...*, 2010).

Order Phasmatida. Family Permophasmatidae (Gorochov, 1992)

Normandien. South African Republic, KwaZulu-Natal Province, group of localities in the Karoo and Lebombo river basins near the Drakensberg Mountains (Bulver, KwaYaya, Clouston Farm, Lidgetton, Mount West, Mooi River, Far End, Emakwezini, etc.); Upper Permian, Changhsingian or Wuchiapingian Stage, Karoo Supergroup, Beaufort Group, Adelaide Subgroup, Normandien Formation, equivalent of Emakwezini Formation (Aristov et al., 2009a; Prevec et al., 2009). Judging from the insect assemblage (see below), the deposits belong to the Severodvinian Stage. A total of about 250 specimens have been collected, stored in the Natal Museum and in the Bernard Price Institute (M.B. Mostovski, pers. comm.).

Order Odonata. Families Ditaxineuridae and Permolestidae (L.N. Pritykina, pers. comm.).

Order Diaphanopterida. Family Scytohymenidae (Chapter 2.2).

Order Hemiptera. Families Prosbolidae, Protopsyllidiidae, Dunstaniidae, Ignotalidae (Shcherbakov, 2000), Dysmorphoptilidae (Shcherbakov, 1984), and Scytinopteridae (D.E. Shcherbakov, pers. comm., for *Afrostenovicia* Dijk et Geertsema, 1999).

Order Paleomanteida. Families Paleomanteidae (Dijk and Geertsema, 1999) and Permosialidae (Rasnitsyn and Dijk, 2011).

Order Coleoptera. Families Rhombocoleidae, Schizocoleidae, Permosynidae, and Taldycupedidae (Ponomarenko and Mostovski, 2005).

Order Neuroptera. Families Permithonidae and Archeosmylidae (Dijk and Geertsema, 1999).

Order Panorpida. Family Permochoristidae (Novokshonov, 1997).

Order Trichoptera. Families Protomeropidae (Sukacheva et al., 2007) and Cladochoristidae (Chapter 2.5).

Order Grylloblattida. Families Chauliodititidae, Liomopteridae, Megakhosaridae (Aristov et al., 2009a), and Skaliciidae (D.S. Aristov, unpublished data).

Order Perlida. Families Palaeonemouridae (Dijk and Geertsema, 2004) and Euxenoperlidae (Riek, 1976).

Order Forficulida. Family Permofulgoridae (Rasnitsyn and Quicke, 2002).

Order Orthoptera. Families Pruvostitidae (Gorochov, 1995) and Xenopteridae (Dijk and Gorochov, 2011).

Belmont. Australia, New South Wales, Group of liomopterid localities in the area of Belmont and Warner's Bay north of Sydney (Brown's Outcrop, Burton Road, Croudace Quarry, 205, 206, St. Andrews Park, etc.); Upper Permian, lower layers of the Changhsingian Stage (Shi et al., 2010), Sydney Basin, Upper Newcastle Coal Measures, upper part of the Croudace Bay Formation, Belmont Conglomerate Member. Judging from the insect assemblage (see below), these deposits belong to the Vyatkian Stage. A total of at least 2000 insect specimens have been collected, stored in the Australian Museum, Sydney, Australia, and in the Natural History Museum, London, United Kingdom (Beattie, 2007).

Order Odonata. Family Permaeshnidae (Jell, 2004).

Order Hypoperlida. Family Ischnoneuridae (Rasnitsyn and Aristov, 2012; Chapter 2.1).

Order Psocida. Family Psocidiidae (Jell, 2004).

Order Tripida. Family Lophioneuridae (Jell, 2004).

Order Hemiptera. Families Archescytinidae, Prosbolidae, Protopsyllidiidae, Dysmorphoptilidae, Dunstaniidae, Stenoviciidae, Paraknightiidae, Progonocimicidae, Pincombeidae (Shcherbakov, 2000), and Simulaphididae (Shcherbakov, 2007).

Order Palaeomanteida. Family Permosialidae (Riek, 1968).

Order Coleoptera. Families Rhombocoleidae, Permosynidae (Ponomarenko, 2004), and Asiocoleidae (A.G. Ponomarenko pers. comm.).

Order Neuroptera. Families Permithonidae and Archeosmylidae (Ponomarenko and Shcherbakov, 2004).

Order Jurinida. Family Jurinidae (Jell, 2004).

Order Panorpida. Families Permochoristidae, Belmontiidae, Robinjohniidae, Permotipulidae, Permotanyderidae, Parachoristidae (Novokshonov, 1997), and Mesopsychidae (Bashkuev, 2011b).

Order Trichoptera. Family Protomeropidae (Novokshonov, 1997), Cladochoristidae (Chapter 2.5).

Order Grylloblattida. Families Liomopteridae and Sylvaphlebiidae (Aristov, 2009b).

Order Perlida. Family Eustheniidae (Chapter 2.7).

Order Forficulidae. Family Dermelytridae and Permofulgoridae (Rasnitsyn and Quicke, 2002).

Intertrappean Deposits of the Tunguska Basin

Intertrappean deposits of the Tunguska Basin (Central Siberian Plateau, Krasnoyarsk Region, Evenkiiskii District) belong to four horizons: Tutonchanian (the earliest), Lebedevskian, Khungtukunian

(Korvunchana Group), and Putoranian (Putorana Group) (Sadovnikov and Orlova, 1995). Insects have been found in the last three horizons. The correlation of these horizons with other regions and with the General Stratigraphic Chart is controversial. Some authors attribute the intertrappean deposits to the Upper Permian (Meyen, 1992; Sadovnikov and Orlova, 1994). Sadovnikov and Orlova (1994) attribute the Tutonchanian and Lebedevskian horizons to the Vyatkian Stage and the Khungtukunian and Putoranian horizons to the "Taimyrian" Stage, the terminal stage of the Permian. At the same time, a part of the Putoranian Horizon corresponds to the lower portion of the Vokhma Formation (Nedubrovo and Astashikha members) of European Russia (Sadovnikov, 2009). According to all officially approved stratigraphic scales, these deposits belong to the Triassic. In the opinion of Mogucheva and Kruglovykh (2009), the lower layers of the Dvurogian (=Lebedevskian) Horizon correspond to the upper layers of the Induan and the lower layers of the Olenekian; the upper layers of the Dvurogian (=Khungtukunian) Horizon and the lower layers of the Putoranian Horizon correspond to the Olenekian Stage; and the upper layers of the Putoranian Horizon correspond to the Anisian Stage. In the above-mentioned study, the lower layers of the Dvurogian (=Lebedevskian) Horizon are correlated with the Kedrovyi beds of the Mal'tsevo Formation of the Kuznetsk Basin (Babii Kamen' locality).

At the same time, the most reliable currently available absolute dates point not only to a relatively short period of the outflow of the Siberian traps (less than two million years), but also to the termination of their main phase about 250.3 ± 1.1 Ma, i.e., before the officially accepted Permian–Triassic boundary (249.25 ± 0.14 million years; Reichow et al., 2009). This circumstance suggests that intertrappean assemblages were approximately contemporaneous and, thus, they are analyzed jointly, primarily because assemblages from different horizons are rather similar and, what is more important, they are too poor and nonrepresentative separately, but taken together provide rather definite information. Therefore, at the present level of knowledge of these deposits, such a generalized analysis is justified.

The Lebedevskian Horizon is represented by the localities of **Anakit** (three localities on the Lower Tunguska River near the mouth of the Anakit River; Chichikan Formation) and **Bugarkita-1** (=Nizhnyaya Bugarikhta; Bugarikta River (left tributary of the Tutonchana River 30 km upstream from its mouth), 1 km from the mouth; Bugarikta Formation). The Lebedevskian or Khungtukunian Horizon is represented by the intertrappean locality of **Malaya Kheta** (=Arktika, =Ust'-Port; Taimyrskii District, left bank of the Yenisei River near the mouth of the Malaya Kheta River, 120 km northwest of Dudinka). The Khungtukunian Horizon is represented by **Khungtukun-2** and **Khungtukun-4** (right bank of the Lower Tunguska River, 4.9 km and 3.1 km, respectively, east of the mouth of the Khungtukun River; Pirda Formation) and, probably, by **Nizhnyaya Lyulyuikta-**1 (left bank of the Lower Tunguska River, 3.2 km west-southwest of the mouth of the Nizhnyaya Lyulyuikta River; upper layers of the Lebedevskian Horizon or lower layers of the Khungtukunian Horizon). The Putoranian Horizon is represented by **Severnoe** (southern shore of Lake Severnoe opposite the mouth of the Epekli-Sen River; Nidym Formation), **Untuun-2** (Lower Tunguska River Basin, left bank of the Untuun River, left bank of the Kochechumo River, 15 km from the mouth, or 10 km by a straight line, opposite the mouth of the Khoktokon River; Kochechumo Formation), **Nikungdakan-1** (=Tura; Lower Tunguska River Basin 33 km east-southeast of the village of Tura, left bank of the Nirungdakan River, 10 km from its mouth; Agitnak Formation), and **Ukshunukan-2** (=Ilimpeya; right bank of the middle reaches of the Ilimpeya River, 3.3 km downstream from the Ukshunukan River; Limptekon Formation).

A total of 600 insect specimens, stored in PIN, have been collected in these localities. A combined list of the families identified from these localities is given below.

Order Ephemerida. Families Sharephemeridae (Khungtukun-2) and Vogesonymphidae (Khungtukun-2, Khungtukun-4) (Sinitshenkova, 2013).

Order Hemiptera. Families Archescytinidae (Niznyaya Bugarikhta), Stenoviciidae (Khungtukun-2), Surijokocixiidae (Ust'-Port), and Ignotalidae (Ukshunukan, Severnoe, Khungtukun-2) (Shcherbakov, 2000; D.E. Shcherbakov, pers. comm.).

Order Coleoptera. Families Taldycupedidae (Ukshunukan), Schizocoleidae (Anakit, Ukshunukan), Permosynidae (Anakit, Lyulyuikta, Khungtukun, Anakit), Asiocoleidae (Anakit), Triaplidae (Anakit), and Trachypachidae (Anakit) (A.G. Ponomarenko, pers. comm.).

Order Neuroptera. Family Permithonidae (Ukshunukan; Ponomarenko and Shcherbakov, 2004).

Order Panorpida. Families Mesopsychidae (Khungtukun-2), Nedubroviidae (Lyulyuikta), and Permotanyderidae (Niznyaya Bugarikhta, Lyulyuikta) (Bashkuev, 2013).

Order Blattida. Family Phyloblattidae (Vršanský, 2010b).

Order Grylloblattida. Families Chauliodititidae (Anakit, Khungtukun), Geinitziidae (Malaya Lyulyuikta), Megakhosaridae (Anakit), Blattogryllidae (Anakit) (Aristov, 2011).

Order Orthoptera. Family Locustavidae (Niznyaya Bugarikhta; Sharov, 1968).

Babii Kamen'. Russia, Kemerovo Region, Novokuznetskii District, right bank of the Tom River, 10 km downstream from the city of Ust'-Naryk; Aba Group, Mal'tsevo Formation, Kedrovyi beds. A total of 138 specimens have been collected, stored in PIN. The age of the insect-bearing beds corresponds to the Induan Stage (Shcherbakov et al., 2002). According to an opposite point of view (Mogucheva and Kruglovykh, 2009), the Kedrovyi beds are correlated with the lower layers of the Dvurogian (=Lebedevskian) Horizon, which correspond to the upper layers of the Induan and the lower layers of the Olenekian. According to the latest, most reliable data of the Ar-Ar isotope method, the Permian–Triassic boundary lies at 249.25 ± 0.14 Ma (Reichow et al., 2009), and runs in the Kuznetsk Basin in the upper part of the Mal'tsevo Formation, upward in the section from the position of the Karaganskii sill (250.3 ± 0.7–250.7 ± 0.6) and Syrkashevskii sill (252.2 ± 0.5–252.3 ± 0.6: Buslov et al., 2010). According to Shcherbakov et al. (2002), the insect-bearing beds lie lower in the section. Thus, the age of insects of Babii Kamen' and that of intertrappean Siberian assemblages is technically estimated as approximately the same, terminal Permian. Biogeographically, Babii Kamen' was situated at that time at a higher paleolatitude than Tunguska, in the cold–temperate climatic zone rather than in the temperate semiarid zone, to which Tunguska belonged (Shcherbakov, 2009).

The following insects have been collected in Babii Kamen':

Order Ephemerida. Family Misthodotidae (Shcherbakov et al., 2002).

Order Hemiptera. Families Prosbolidae, Scytinopteridae, and Hylicellidae (Shcherbakov et al., 2002).

Order Coleoptera. Families Schizocoleidae, Ademosynidae (as Permosynidae in Table 1, text-fig. 1, and calculations), Triaplidae, Trachypachidae, Hydrophilidae, and Byrrhidae (Ponomarenko, 2004).

Order Neuroptera. Family Archeosmylidae (Ponomarenko and Shcherbakov, 2004).

Order Panorpida. Family Mesopsychidae (Bashkuev, 2011b).

Order Blattida. Families Subioblattidae and Blattulidae (P. Vršanský, pers. comm.).

Order Grylloblattida. Families Chauliodititidae (Aristov, 2003), Geinitziidae (Aristov, 2004).

Order Orthoptera. Family Mesoedischiidae (Gorochov, 2005a).

Structure and Dynamics of Insect Diversity in the Period Studied

To date, a total of 25 orders and 115 families of insects have been found in deposits of the terminal Permian (Urzhumian to Vyatkian) and Lower Triassic. Particular finds of families and their general distribution, along with similar data on other, better studied regions of the planet, are given in Table 2 and Figs. 91 and 92. Calculations based on these data are shown in Tables 3–14 and Figs. 93–95. The results allow discussing some aspects of the insect diversity dynamics during this period. However, first we have to substantiate the methodological approaches we used.

3.1.2. Methods

The analysis of distribution and taxonomic dynamics is performed here based on the data on insect families and their distribution over particular localities or, in some cases, groups of presumably contemporaneous localities of limited geographic distribution. The taxonomic level of families is generally accepted as optimal for such purposes and scarcely requires additional substantiation. The analysis of particular localities rather than successive stratigraphic units is connected with continuing heated debates on the correctness of various methods for analyzing such data (cf. Rasnitsyn, 2005, and Dmitriev and Ponomarenko, 2009). The use of particular local assemblages does not imply such problems, but it is not free from other difficulties. The most important of them is the necessity to arrange the analyzed assemblages in a linear sequence, even if there is not enough stratigraphic grounds for such an ordination. This problem can be solved to some extent by comparison of several alternative sequences (see below).

The initial stratigraphic sequence of assemblages used here (Table 3) mostly follows Shcherbakov (2008). The Permian–Triassic insect assemblages from the intertrappean deposits of Tunguska, which were not discussed there, are taken for a single combined assemblage, because the presumably short duration of the trappean outflows in Siberia suggests that these assemblages are close in age (see above), their composition at the family level is rather uniform, and the amount of material from each formation is insufficient for calculations. The position immediately before Vyazniki of the Aristovo assemblage, which is also not included in the Shcherbakov's sequence, directly follows from the results given in Chapter 1.

Tables 3–8, 10–12, 14, show the data on particular assemblages, including the total number of specimens, the number of first and last appearances of families in the fossil record, and the number of families in some other categories. These categories include (1) *transitional* families (those that emerged before the Urzhumian and survived until at least the Middle Triassic); (2) families that emerged **before the Urzhumian** and did not survive through the Lower Triassic, hereinafter called *conditionally considered Paleozoic* or simply *ancient* (strictly in this context); (3) families that emerged **not earlier than the Urzhumian** and survived through the Lower Triassic, hereinafter called *conditionally considered post-Paleozoic* or *young*; and (4) families *conditionally considered endemic* to the period in question (those that emerged not earlier than the Urzhumian and became extinct not later than the Early Triassic).

To provide at least a rough estimate of the direction and rate of the faunal renewal, we included in the

Table 2. Insect families found in the Urzhumian-Induan and their complete distribution. References: [1] Engel (2009); [2] Bashkuev et al (2012); [3] Sinitshenkova and Vassilenko (2011); [4] Rasnitsyn and Quicke (2002); [5] Brauckmann (1991); [6] Tillyard (1926); [7] Pritykina (1981); [8] Tillyard (1926); [9] Rasnitsyn et al. (2004); [10] Carpenter (1992); [11] Kukalová-Peck (1972); [12] Vishniakova (1981); [13] Shcherbakov (2000); [14] Shcherbakov (2008); [15] Shcherbakov (pers. comm.); [16] Shcherbakov (1988); [17] Shcherbakov (2007); [18] Katalog kollektsii ... (2010); [19] Aristov and Rasnitsyn (2009); [20] Ponomarenko (2000b); [21] Ponomarenko (1969); [22] Tan et al. (2009); [23] Ponomarenko (pers. comm.); [24] Ponomarenko (1977); [25] Ponomarenko and Shcherbakov (2004); [26] Rohdendorf et al. (1961); [27] Novokshonov (1997); [28] Novokshonov and Sukacheva (2001); [29] Aristov (2009b); [30] Vishniakova (1998); [31] Martins-Neto et al. (2005); [32]); Vršanský (pers. comm.); [33] Vršanský (2008); [34] Schneider (1983); [35] Papier and Grauvogel-Stamm (1995); [36] Vršanský (2003); [37] Storozhenko (1997); [38] Béthoux and Beckemeyer (2007); [39] Aristov et al. (2009); [40] Aristov et al. (2009); [41] Aristov (2005); [42] Storozhenko (1998); [43] Aristov (2011a); [44] Aristov (2004d); [45] Aristov (2012); [46] Sinitshenkova (1987); [47] Gorochov (2005a); [48] Gorochov (1995); [49] Gorochov (2005b); [50] Gorochov (pers. comm.); [51] Dijk and Gorochov (2011); [51] Dijk and Gorochov (2011); [52] Sinitshenkova (2012). No reference is given to the records considered above in this publication

Family	First appearance	Occurrence in localities analyzed	Last appearance
Dasyleptidae	C_3st [1]	Isady	T_2 ani [2]
Protereismatidae	P_1sk [3]	Isady	Isady
Misthodotidae	P_1 ar [4]	Isady, Babii Kamen’	T_2 [3]
Sharephemeridae	Khungtukun [52]	Khungtukun-2 [52]	J_3 [52]
Vogesonymphidae	Khungtukun [52]	Khungtukun-2, -4 [52]	T_2 [52]
Meganeuridae	C_2b [5]	Kargala, Karaungir, Novo-Aleksandrovka	Novo-Aleksandrovka
Kennedyidae	P_1 ar [6]	Isady	T_3 [7]
Ditaxineuridae	P_1 ar [8]	Bor-Tologoi, Normandien	Normandien
Permolestidae	P_1kg [4]	Kargala, Isady, Normandien	Normandien
Caloneuridae	C_2 [4]	Kargala, Bor-Tologoi, Isady	Isady
Ischnoneuridae	C_2 [4]	Chepanikha, Isady, Belmont	Belmont
Tococladidae	P_1ar	Kargala	Kargala
Hypoperlidae	P_1kg [4]	Isady	Isady
Mongolodictyidae	Bor-Tologoi	Bor-Tologoi	Bor-Tologoi
Calvertiellidae	C-P [9]	Isady	Isady
Scytohymenidae	P_1kg [10]	Normandien	Normandien
Moravohymenidae	P_1sk [11]	Isady	Isady
Psocidiidae	P_1 sk [4]	Isady, Belmont, Nedubrovo	Nedubrovo
Lophioneuridae	P_1 ar [12]	Suriekovo, Karaungir Isady, Belmont, Sokovka, Balymotikha	K_2st [10]
Archescitinidae	P_1sk [13]	Suriekovo, Bor-Tologoi, Karaungir, Belmont, Nedubrovo, Nizhnyaya Bugarikhta	Nizhnyaya Bugarikhta
Boreoscytidae	P_1kg [13]	Bor-Tologoi	Bor-Tologoi
Coleoscytidae	P_1kg [13]	Bor-Tologoi	Bor-Tologoi
Prosbolopseidae	P_1kg [13]	Bor-Tologoi, Novo-Aleksandrovka, Karaungir	Karaungir
Prosbolidae	P_2kz^1 [13]	Chepanikha, Suriekovo, Sokolova, Bor-Tologoi, Novo-Aleksandrovka, Karaungir, Isady, Normandien, Belmont, Balymotikha, Babii Kamen'	Babii Kamen'
Ingruidae	P_1kg [13]	Chepanikha, Novo-Aleksandrovka, Bor-Tologoi, Karaungir Isady	Belmont
Scytinopteridae	P_2kz^1 [13]	Chepanikha, Suriekovo, Sokolova, Bor-Tologoi, Novo-Aleksandrovka, Karaungir Isady, Normandien, Balymotikha, Nedubrovo, Babii Kamen', Khungtukun-2	K_1 [13]
Stenoviciidae	P_3sv [13]	Bor-Tologoi, Novo-Aleksandrovka, Isady, Aristovo, Balymotikha, Belmont, Khungtukun-2	T_{2-3} [13]
Pereboriidae	P_2kz^1 [13]	Chepanikha, Kargala, Bor-Tologoi, Novo-Aleksandrovka, Isady, Balymotikha, Karaungir	Karaungir
Surijokocixiidae	Chepanikha	Chepanikha, Suriekovo, Kargala, Novo-Aleksandrovka, Balymotikha, Nedubrovo, Ust’-Port, Khungtukun-2	T_3 [13]
Serpentivenidae	Chepanikha	?Chepanikha, Suriekovo, Karaungir	T_{2-3} [13]
Dunstaniidae	Bor-Tologoi	Bor-Tologoi, Karaungir, Isady, Normandien, Belmont, Aristovo, Balymotikha	J_1 [13]
Ignotalidae	P_2sd^2 [14]	Normandien, Ukshunukan, Severnoe	$T_{2/3}$ [15]
Dysmorphoptilidae	P_2kz^1 [13]	?Chepanikha, Novo-Aleksandrovka, Karaungir, Isady, Sokolova, Normandien, Belmont, Balymotikha	J_1 [13]
Paraknightiidae	Sokolova	Sokolova, Belmont, Balymotikha	T_{2-3} [13]
Hylicellidae	Babii Kamen’	Babii Kamen’	K_1 [16]
Progonocimicidae	Isady	Isady, Belmont, Balymotikha, Nedubrovo	K_1[4]

Table 2. (Contd.)

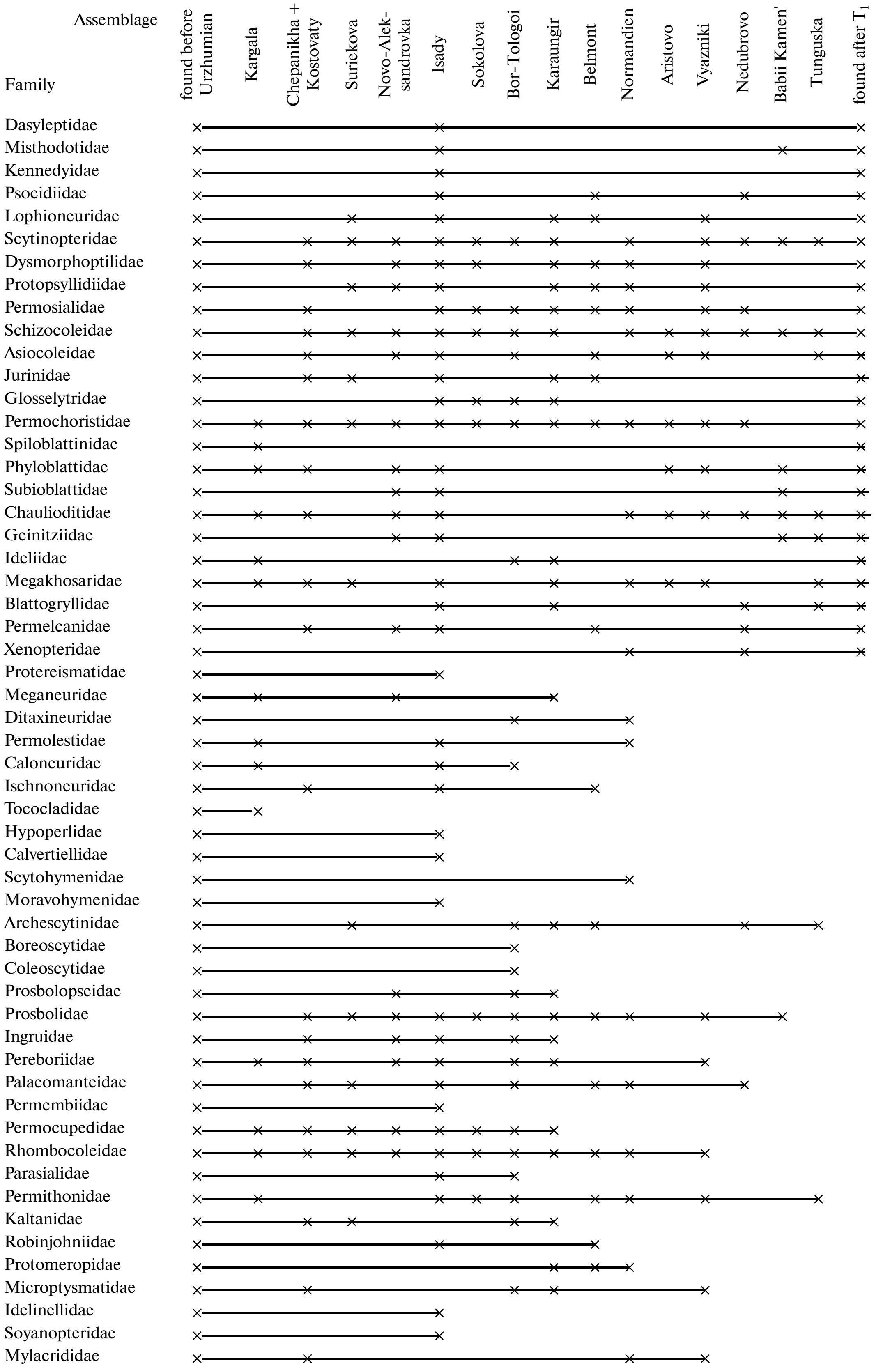
Family	First appearance	Occurrence in localities analyzed	Last appearance
Pincombeidae	Belmont	Belmont	T_3 [13]
Protopsyllidiidae	P_2kz^1 [4]	Suriekovo, Karaungir, Normandien, Belmont, Novo-Aleksandrovka, Isady, Balymotikha	K_2 [13]
Simulaphididae	Belmont	Belmont	?T_3 [17]
Paleomanteidae	C_2 [9]	Chepanikha, Suriekovo, Bor-Tologoi, Isady, Normandien, Nedubrovo	Isady
Permosialidae	P_1sk	Chepanikha, Kostovaty, Sokolova Bor-Tologoi, Isady, Normandien, Karaungir, Belmont, Balymotikha, Nedubrovo	Karatau [18]
Permembiidae	P_1 ar [19]	Isady	Isady
Permocupedidae	P_2kz^1 [20]	Chepanikha, Suriekovo, Kargala, Karaungir, Novo-Aleksandrovka, Sokolova, Bor-Tologoi, Isady	T_2 Franconia [23]
Rhombocoleidae	P_2kz^2 [4]	Chepanikha, Kostovaty, Suriekova, Kargala, Novo-Aleksandrovka, Sokolova, Bor-Tologoi, Isady, Normandien, Karaungir, Belmont, Balymotikha	Belmont
Schizocoleidae	P_2kz^2 [4]	Chepanikha (as Schizophoridae), Suriekovo, Novo-Aleksandrovka, Sokolova, Bor-Tologoi, Isady, Normandien, Aristovo, Karaungir, Balymotikha, Nedubrovo, Entala, Babii Kamen', Anakit, Ukshunukan	J_2 [21]
Permosynidae	Kul'chumovo	Sokolova, Normandien, Aristovo, Belmont, Sokovka, Balymotikha, Babii Kamen', Anakit, Lyulyuikta, Khungtukun	K_1 [21]
Taldycupedidae	Kargala	Kargala, Suriekovo, Sokolova, Bor-Tologoi, Isady, Normandien, Karaungir, Nedubrovo, Ukshunukan, Anakit, Khungtukun	T.$_3$ [21]
Asiocoleidae	P_2kz^2 [4]	Kostovaty, Novo-Aleksandrovka, Bor-Tologoi, Isady, Aristovo, Belmont, Balymotikha, Anakit	J_2 [22 as Tricoleidae]
Triaplidae	Babii Kamen'	Babii Kamen', Anakit	T_3 [23]
Trachypachidae	Babii Kamen'	Babii Kamen', Anakit	Recent
Hydrophilidae	Babii Kamen'	Babii Kamen'	Recent
Byrrhidae	Babii Kamen'	Babii Kamen'	Recent
Parasialidae	Soyana [24]	Bor-Tologoi, Isady	Isady
Permithonidae	P_1sk [4]	Kargala, Bor-Tologoi, Sokolova, Isady, Normandien, Belmont, Balymotikha, Ukshunukan	Ukshunukan
Archeosmylidae	Belmont	Normandien, Belmont, Babii Kamen'	T_3 [25]
Jurinidae	P_2kz^1	Chepanikha, Suriekovo, Isady, Karaungir, Belmont	J_1
Glosselytridae	P_1 kg	Karaungir, Bor-Tologoi, Isady, Sokolova,	T_3
Kaltanidae	P_2kz^2 [26]	Chepanikha, Suriekovo, Bor-Tologoi, Karaungir	Karaungir
Permochoristidae	P1ar [8]	Chepanikha, Kostovaty, Kargala, Suriekovo, Bor-Tologoi, Novo-Aleksandrovka, Sokolova, Isady, Normandien, Aristovo, Karaungir, Belmont, Balymotikha, Nedubrovo	J [27]
Mesopsychidae	Isady	Isady, Belmont, Sokovka, Balymotikha, Nedubrovo, Babii Kamen', Khungtukun-2	K_1 [28]
Nedubroviidae	Isady	Isady, Sokovka, Balymotikha, Nedubrovo, Lyulyuikta	Lyulyuikta
Belmontiidae	Belmont	Belmont	Belmont
Robinjohniidae	$P_{1?}$ [27]	Isady, Belmont	Belmont
Permotipulidae	Suriekovo	Suriekovo, Belmont	Belmont
Permotanyderidae	Isady	Isady, Aristovo, Belmont, Nedubrovo Nizhnyaya Bugarikhta, Lyulyuikta	Nizhnyaya Bugarikhta
Parachoristidae	Belmont	Belmont	T_3 [27]
Protomeropidae	P_1sk	Normandien, Karaungir, Belmont	Belmont
Microptysmatidae	P_1sk	Chepanikha, Kostovaty, Bor-Tologoi, Karaungir, Balymotikha	Balymotikha
Cladochoristidae	Isady	Isady, Normandien, Belmont, Balymotikha	T_3 [27]
Prorhyacophilidae	Balymotikha	Balymotikha	T_3 [27]
Idelinellidae	P_1kg [29]	Isady	Isady
Soyanopteridae	P_1kg	Isady	Isady
Mylacrididae	C_2 [4]	Chepanikha, Normandien, Balymotikha	Balymotikha
Spiloblattinidae	C_2 [4]	Kargala	$T_{2/3}$ [30]

Table 2. (Contd.)

Family	First appearance	Occurrence in localities analyzed	Last appearance
Argentinoblattidae	Novo-Aleksandrovka	Novo-Aleksandrovka, Isady, Sokovka, Balymotikha, Nedubrovo	T_3 [31]
Mutoviidae	Isady	Isady, Aristovo, Balymotikha	Balymotikha
Caloblattinidae	Kul'chumovo	Isady	K_1 [32]
Phyloblattidae	C_2 [4]	Chepanikha, Kargala, Novo-Aleksandrovka, Isady, Aristovo, Balymotikha, Entala, Nizhnyaya Bugarikhta	K_1apt [33]
Subioblattidae	P_1sk [34]	Novo-Aleksandrovka, Isady, Babii Kamen'	T_2lad [35]
Blattulidae	Babii Kamen’	'Babii Kamen'	K_1 [36]
Cacurgidae	C_2 [45]	Isady	Isady
Permulidae	P_1 [37]	Chepanikha, Isady	Isady
Tshekardominidae	P_1ar [38]	Chepanikha, Bor-Tologoi, Karaungir, Novo-Aleksandrovka	Novo-Aleksandrovka
Chauliodititidae	P_2kz^2 [39]	Chepanikha, Kargala, Novo-Aleksandrovka, Isady, Normandien, Aristovo, Sokovka, Balymotikha, Entala, Nedubrovo, Babii Kamen', Tikhvinskoe, Anakit, Khungtukun	T_2 [2]
Geinitziidae	P_2kz^2 [39]	Novo-Aleksandrovka, Isady, Babii Kamen', Malaya Lyuluyikta	J_3 [40]
Lemmatophoridae	C-P [9]	Kostovaty	Kostovaty
Liomopteridae	C-P [9]	Chepanikha, Kostovaty, Kargala, Suriekovo, Bor-Tologoi, Novo-Aleksandrovka, Isady Normandien, Aristovo, Belmont	Belmont
Ideliidae	P_1kg [29]	Kargala, Bor-Tologoi, Karaungir	T_3 [41]
Skaliciidae	P_1sk [52]	Kargala, Normandien	Normandien
Megakhosaridae	P_1kg [29]	Chepanikha, Kargala, Suriekovo, Isady, Normandien, Aristovo, Karaungir, Balymotikha, Anakit	$T_{2/3}$ [42]
Blattogryllidae	P_2kz^2 [43]	Karaungir, Isady, Nedubrovo, Anakit	K_1 [42]
Kortchakoliidae	P_1kg [29]	Isady	Isady
Tunguskapteridae	P_3 sd [29]	Isady	$T_{2/3}$ [42]
Kargalopteridae	Kargala	Kargala	Kargala
Sylvaphlebiidae	P_1sk [44]	Belmont	Belmont
Permothermopsidae	P_1kg [29]	Isady, Karaungir	Karaungir
Mesorthopteridae	Isady	Isady	T_3 [10]
Tshekardoperlidae	P_1kg [46]	Isady	Isady
Palaeonemouridae	P_2kz^2 [46]	Chepanikha, Kargala, Bor-Tologoi, Novo-Aleksandrovka, Isady, Normandien, Karaungir, Aristovo	Karaungir
Palaeoperlidae	P_2kz^2 [46]	Kargala, Novo-Aleksandrovka, Isady, Karaungir	Isady
Euxenoperlidae	Isady	Isady, Normandien	T_3 [46]
Eustheniidae	Isady	Isady, Belmont	Recent
Dermelytridae	Bor-Tologoi	Bor-Tologoi, Isady, Belmont	Belmont
Permofulgoridae	P_2kz^1 [4]	Normandien, Belmont	Belmont
Mesoedischiidae	Babii Kamen'	Babii Kamen’	T_{2-3} [47]
Pruvostitidae	P_1kg [48]	Kargala, Isady, Normandien	Normandien
Oedischiidae	C_3[NB]	Chepanikha	Chepanikha
Permelcanidae	P_1ar [48]	Chepanikha, Novo-Aleksandrovka, Isady, Nedubrovo	$T_{2/3}$ [48]
Locustavidae	Belmont	Belmont, Nizhnyaya Bugarikhta	T_{2-3} [49]
Proparagryllacrididae	Isady	Isady	T_{2-3} [49]
Xenopteridae	Soyana [50]	Normandien	T_3 [51]
Permophasmatidae	Bor-Tologoi	Bor-Tologoi, Isady	Isady
Deinotitanidae	Novo-Aleksandrovka	Novo-Aleksandrovka, Isady, Balymotikha	Balymotikha
Homoeodictyidae	Kargala	Kargala	Kargala
Alexarasniidae	Isady	Isady	Isady

Table 3. Initial sequence of assemblages (sum of gaps 661). Families conditionally considered Paleozoic are those the first appearance of which is earlier than the Urzhumian and the last appearance of which is not later than the Induan; families conditionally considered post-Paleozoic are those the first appearance of which is not earlier than the Urzhumian and the last appearance of which is later than the Induan; families provisionally considered endemic of the Urzhumian-Induan are those the first and last appearances of which fall in this period; $\ln_{total}$ is natural logarithm of the total number of insect specimens in the assemblage; Pz/pPz is the ratio of the number of families provisionally considered Paleozoic and post-Paleozoic; turnover (measure of faunal renewal) is the sum of first and last appearances normalized by the logarithm of the number of specimens

Assemblage	Kargala	Chepanikha + Kostovaty	Suriekova	Novo-Aleksandrovka	Isady	Sokolova	Bor-Tologoi	Karaungir	Belmont	Normandien	Aristovo	Vyazniki	Babii Kamen'	Tunguska	Nedubrovo
Total number of specimens	300	400	670	300	3500	570	900	550	2000	250	250	350	140	600	200
Ln_{total}	5.7	6.0	6.5	5.7	8.2	6.3	6.8	6.3	7.6	5.5	5.5	5.9	4.9	6.4	5.3
Total number of families	23	29	18	26	69	13	32	31	37	30	13	30	18	22	18
Families/$\ln_{total}$	4.0	4.7	2.8	4.6	8.6	2.1	4.4	4.9	4.9	5.5	2.5	5.2	3.7	3.1	3.6
Number of first appearances	4	1	1	3	16	2	1	0	6	1	0	1	7	2	0
First/$\ln_{total}$	0.7	0.3	0.1	0.5	1.6	0.3	0.7	0	0.8	0.2	0	0.2	1.6	0.3	0
Number of last appearances	3	2	0	0	12	0	6	7	6	7	2	6	1	1	4
Last/$\ln_{total}$	0.5	0.3	0	0	1.7	0	0.9	1.1	1.2	0.3	0.2	1.2	0.2	0.2	0.7
Number of transitional	7	12	8	12	22	7	8	13	9	9	6	11	7	7	9
Number of transitional/$\ln_{total}$	1.2	2.0	1.2	2.1	2.7	1.1	1.2	2.1	1.2	1.6	1.1	1.9	1.4	1.1	1.7
Number of Paleozoic	12	14	6	10	26	3	18	15	11	14	2	6	1	2	2
Number of Paleozoic/$\ln_{total}$	2.1	2.3	0.9	1.7	3.2	0.5	2.6	2.4	1.4	2.3	0.4	1.0	0.2	0.3	0.4
Number of post-Paleozoic	2	2	3	3	13	3	3	3	13	7	3	10	10	11	5
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	0.5	1.6	0.5	0.4	0.5	1.7	1.3	0.5	1.7	2.0	1.7	0.9
Number of endemics	2	0	1	1	7	0	3	0	4	0	2	3	0	2	2
Endemics/$\ln_{total}$	0.3	0	0.1	0.2	0.8	0	0.4	0	0.5	0	0.4	0.5	0	0.3	0.4
First/last	1.3	0.5	/0	/0	1.3	/0	0.2	0	1.0	0.1	0	0.2	7.0	2.0	0
Pz/pPz	6.0	7.0	2.0	3.3	2.0	1.0	6.0	5.0	0.8	2.0	0.7	0.6	0.1	0.2	0.4
Turnover	1.2	0.5	0.1	0.5	3.4	0.3	1.0	1.1	1.6	1.5	0.4	1.2	1.6	0.5	0.7



Assemblage Family	found before Urzhumian	Kargala	Chepanikha + Kostovaty	Suriekova	Novo-Aleksandrovka	Isady	Sokolova	Bor-Tologoi	Karaungir	Belmont	Normandien	Aristovo	Vyazniki	Nedubrovo	Babii Kamen'	Tunguska	found after T_1
Dasyleptidae	×					×											×
Misthodotidae	×					×									×		×
Kennedyidae	×					×											×
Psocidiidae	×					×				×				×			×
Lophioneuridae	×			×		×			×	×			×				×
Scytinopteridae	×		×	×	×	×	×	×	×		×		×	×	×	×	×
Dysmorphoptilidae	×		×		×	×	×		×	×	×		×				×
Protopsyllidiidae	×			×	×	×			×	×	×		×				×
Permosialidae	×		×			×	×	×	×	×	×		×	×			×
Schizocoleidae	×		×	×	×	×	×	×	×		×	×	×	×	×	×	×
Asiocoleidae	×		×		×	×		×		×		×	×			×	×
Jurinidae	×		×	×		×			×	×							×
Glosselytridae	×					×	×	×	×								×
Permochoristidae	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×
Spiloblattinidae	×	×															×
Phyloblattidae	×	×	×		×	×						×	×		×		×
Subioblattidae	×				×	×									×		×
Chaulioditidae	×	×	×		×	×					×	×	×	×	×	×	×
Geinitziidae	×				×	×									×	×	×
Ideliidae	×	×						×	×								×
Megakhosaridae	×	×	×	×		×			×		×	×	×			×	×
Blattogryllidae	×					×			×					×		×	×
Permelcanidae	×		×		×	×				×				×			×
Xenopteridae	×										×			×			×
Protereismatidae	×					×											
Meganeuridae	×	×			×				×								
Ditaxineuridae	×							×			×						
Permolestidae	×	×				×					×						
Caloneuridae	×	×				×		×									
Ischnoneuridae	×		×			×				×							
Tococladidae	×	×															
Hypoperlidae	×					×											
Calvertiellidae	×					×											
Scytohymenidae	×										×						
Moravohymenidae	×					×											
Archescytinidae	×			×				×	×	×				×		×	
Boreoscytidae	×							×									
Coleoscytidae	×							×									
Prosbolopseidae	×				×			×	×								
Prosbolidae	×		×	×	×	×	×	×	×	×	×		×		×		
Ingruidae	×		×		×	×		×	×								
Pereboriidae	×	×	×		×	×		×	×				×				
Palaeomanteidae	×		×	×		×		×		×	×			×			
Permembiidae	×					×											
Permocupedidae	×	×	×	×	×	×	×	×	×								
Rhombocoleidae	×	×	×	×	×	×	×	×	×	×	×		×				
Parasialidae	×					×		×									
Permithonidae	×	×				×	×	×		×	×		×			×	
Kaltanidae	×		×	×				×	×								
Robinjohniidae	×					×				×							
Protomeropidae	×								×	×	×						
Microptysmatidae	×		×					×	×				×				
Idelinellidae	×					×											
Soyanopteridae	×					×											
Mylacrididae	×		×								×		×				

Fig. 91. Distribution of insect families over the stratigraphic range under study (initial sequence of assemblages as in Table 3; for explanations, see the text). For sources on each record, see Table 2.

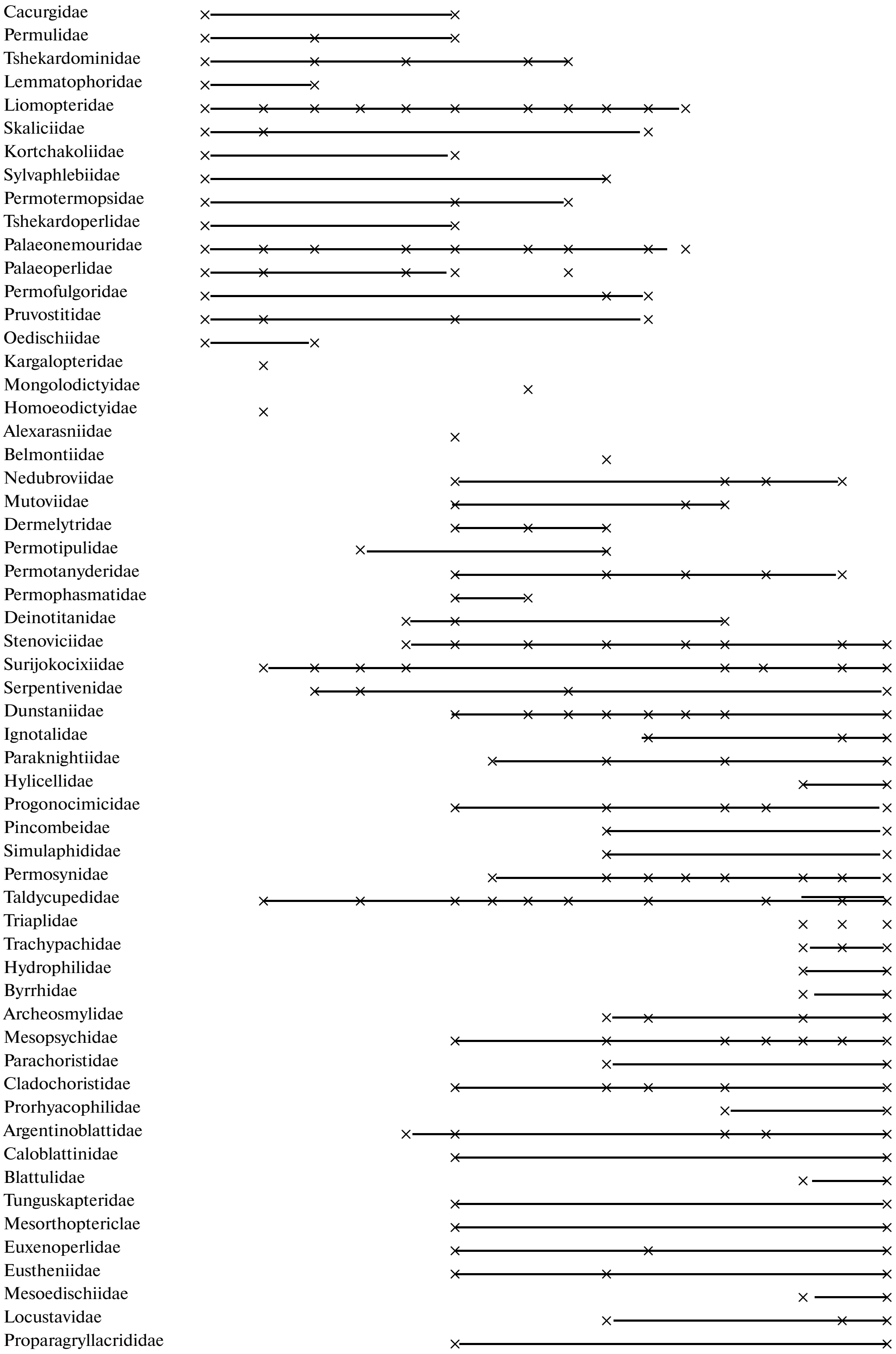

Cacurgidae
Permulidae
Tshekardominidae
Lemmatophoridae
Liomopteridae
Skaliciidae
Kortchakoliidae
Sylvaphlebiidae
Permotermopsidae
Tshekardoperlidae
Palaeonemouridae
Palaeoperlidae
Permofulgoridae
Pruvostitidae
Oedischiidae
Kargalopteridae
Mongolodictyidae
Homoeodictyidae
Alexarasniidae
Belmontiidae
Nedubroviidae
Mutoviidae
Dermelytridae
Permotipulidae
Permotanyderidae
Permophasmatidae
Deinotitanidae
Stenoviciidae
Surijokocixiidae
Serpentivenidae
Dunstaniidae
Ignotalidae
Paraknightiidae
Hylicellidae
Progonocimicidae
Pincombeidae
Simulaphididae
Permosynidae
Taldycupedidae
Triaplidae
Trachypachidae
Hydrophilidae
Byrrhidae
Archeosmylidae
Mesopsychidae
Parachoristidae
Cladochoristidae
Prorhyacophilidae
Argentinoblattidae
Caloblattinidae
Blattulidae
Tunguskapteridae
Mesorthoptericlae
Euxenoperlidae
Eustheniidae
Mesoedischiidae
Locustavidae
Proparagryllacrididae

Fig. 91. (Contd.)

Table 4. Sequence of assemblages optimized by Pz/pPz (sum of gaps 612). For designations, see Table 3

Assemblage	Chepanikha + Kostovaty	Kargala	Bor-Tologoi	Karaungir	Novo-Aleksandrovka	Suriekova	Isady	Normandien	Sokolova	Belmont	Aristovo	Vyazniki	Nedubrovo	Tunguska	Babii Kamen'
Total number of specimens	400	300	900	550	300	670	3500	250	570	2000	250	350	200	600	140
$\ln_{\mathrm{total}}$	6.0	5.7	6.8	6.3	5.7	6.5	8.2	5.5	6.3	7.6	5.5	5.9	5.3	6.4	4.9
Total number of families	29	23	32	31	26	18	69	30	13	37	13	30	18	22	18
Families/$\ln_{\mathrm{total}}$	4.7	4.0	4.4	4.9	4.6	2.8	8.6	5.5	2.1	4.9	2.5	5.2	3.6	3.1	3.7
Number of first appearances	2	3	5	0	2	1	13	3	1	5	0	1	0	4	5
First/$\ln_{\mathrm{total}}$	0.3	0.5	0.7	0	0.3	0.1	1.6	0.5	0.2	0.7	0	0.2	0	0.6	1.0
Number of last appearances	2	3	3	0	3	1	18	5	0	8	2	6	1	4	1
Last/$\ln_{\mathrm{total}}$	0.3	0.5	0.4	0	0.5	0.1	2.2	0.9	0	1.0	0.4	1.0	0.2	0.6	0.2
Number of transitional	12	7	8	13	12	8	22	9	7	9	6	11	9	7	7
Number of transitional/$\ln_{\mathrm{total}}$	2.0	1.2	1.2	2.1	2.1	1.2	2.7	1.6	1.1	1.2	1.1	1.9	1.7	1.1	1.4
Number of Paleozoic	14	12	18	15	10	6	26	14	3	11	2	6	2	2	1
Number of Paleozoic/$\ln_{\mathrm{total}}$	2.3	2.1	2.6	2.4	1.7	0.9	3.2	2.5	0.5	1.4	0.4	1.0	0.4	0.3	0.2
Number of post-Paleozoic	2	2	3	3	3	3	13	7	3	13	3	10	5	11	10
Post-Paleozoic/$\ln_{\mathrm{total}}$	0.3	0.3	0.4	0.5	0.5	0.5	1.6	1.3	0.5	1.7	0.5	1.7	0.9	1.7	2.0
Number of endemics	0	2	3	0	1	1	7	0	0	4	2	3	2	2	0
Endemics/$\ln_{\mathrm{total}}$	0	0.3	0.4	0	0.2	0.1	0.8	0	0	0.5	0.4	0.5	0.4	0.3	0
First/last	1	1	1.7	/0	0.7	1	0.7	0.6	/0	0.6	0	0.2	0	1	5.0
Pz/pPz	7.0	6.0	6.0	5.0	3.3	2.0	2.0	2.0	1.0	0.8	0.7	0.6	0.4	0.2	0.1
Turnover	0.7	1.0	1.2	0	0.9	0.3	3.8	1.5	0.2	1.7	0.4	1.2	0.2	1.2	1.2

tables lines with the same data normalized by the logarithm of the number of fossil specimens collected in each particular locality (i.e., the same values divided by the natural logarithm of the total number of specimens collected in the assemblage). This normalization is based on the fact that the species diversity index, according to which the number of taxa in samples of modern organisms is considered proportional to the logarithm of the sample size ($(S - 1)/\ln N$, where S is the number of taxa in a sample of N specimens), although far from perfect, still "the best of ... the empirical indices" (Pesenko, 1982, p. 60).

The above-mentioned analysis of alternative stratigraphic sequences is aimed at constructing a sequence of assemblages optimal according to certain criteria. The main problems of this task are the choice of optimizing criteria and the ways for exhausting the alternative sequences. We suggest two independent optimality criteria, which should provide a more objective and reliable stratigraphic ordination (ordering) of assemblages. The first criterion, representing the dynamics of the faunal pattern of an assemblage as the ratio of its families conditionally considered Paleozoic (ancient) and post-Paleozoic (young) (Pz/pPz), is a modification of the well-known Lyell's percentage, i.e., the proportion of modern species in the composition of ancient faunas (see Zherikhin, 1978; Rasnitsyn, 1988). This method was some time extremely popular, but the development of other methods for dating and correlating deposits pushed it aside. However, if a sufficient number of orthostratigraphic taxa is absent and applicability of other, more reliable methods is limited (which is generally typical of nonmarine deposits), the use of alternative approaches is justified, as shown below. The ratio Pz/pPz is used for the ordination of insect assemblages characterized in Tables 4, 8, and 12.

The second criterion for ordination is based on the concept of the ghost range, which is useful for similar purposes in different cases (see Rasnitsyn, 2000, 2010). Figures 91 and 92 show that the families studied are not necessarily observed in every assemblage within their stratigraphic range. Each of such gaps is regarded as a single ghost range, during which the taxon in question existed, but has not been found. However, a gap may result not only from the incompleteness of materials, but also from an incorrectly constructed sequence of assemblages, where an earlier or later assemblage in which this taxon is naturally absent (having not yet emerged or already become extinct) is erroneously placed between assemblages where the taxon is present. Rearranging the assem-

Table 5. Complete set of assemblages: initial sequence and ten best sequences of assemblages (sequence of assemblages set in bold type is fixed). First column is the sum of ghost ranges. Designations: (Karg) Kargala, (Ch + Ko) Chepanikha + Kostovaty, (Suri) Suriekova, (N-Alek) Novo-Aleksandrovka, (Isad) Isady, (Soko) Sokolova, (B-Tol) Bor-Tologoi, (Karau) Karaungir, (Belm) Belmont, (Norm) Normandien, (Aris) Aristovo, (Vyaz) Vyazniki, (B-Kam) Babii Kamen', (Tung) intertrappean deposits of the Tunguska, (Nedu) Nedubrovo. First line is the initial sequence, followed by ten sequences ordered by the minimum sum of ghost ranges

661	**Karg**	Ch+Ko	Suri	N-Alek	**Isad**	Soko	B-Tol	Karau	Belm	Norm	Aris	**Vyaz**	B-Kam	Tung	**Nedu**
590	Ch + Ko	**Karg**	Karau	B-Tol	**Isad**	N-Alek	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
592	Ch + Ko	Karau	**Karg**	B-Tol	**Isad**	N-Alek	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
594	Ch + Ko	Karau	B-Tol	**Karg**	**Isad**	N-Alek	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
595	Karau	Ch +Ko	**Karg**	B-Tol	**Isad**	N-Alek	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
597	Karau	Ch +Ko	B-Tol	**Karg**	**Isad**	N-Alek	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
598	Karau	Ch +Ko	B-Tol	N-Alek	**Karg**	**Isad**	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
599	Karau	B-Tol	Ch + Ko	**Karg**	**Isad**	N-Alek	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
600	Karau	B-Tol	Ch + Ko	N-Alek	**Karg**	**Isad**	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
602	Karau	B-Tol	Ch + Ko	N-Alek	**Karg**	**Isad**	Vyaz	Norm	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam
603	Karau	B-Tol	N-Alek	Ch + Ko	**Karg**	**Isad**	Norm	**Vyaz**	Aris	Belm	Suri	**Nedu**	Soko	Tung	B-Kam

blages (changing their sequence), we can try to minimize the number of such cases (i.e., minimize the sum of gaps in the geological history of families) and, thus, approach the true stratigraphic sequence of assemblages. The mutual control of these two criteria of optimal ordination of assemblages is used here to provide more reliable results.

It is impossible to exhaust manually all sequences (if their number is not very small) and this operation requires the development of an appropriate computer program and a computer of sufficient calculating power. Such a program was developed by D.A. Rasnitsyn, who also performed calculations. The program can be briefly described as follows (it is planned to describe it in detail in a separate publication).

The program reads initial data, including the limits (boundary conditions and sequences) from an MS Excel file and, then, generates all possible rearrangements complying with the boundary conditions and, if necessary, with the conditions of the sequence. The last restriction, introduced as an option, means fixation of the sequence of some assemblages in accordance with available geological data in the cases where it is known with certainty that, e.g., Isady is later than Kargala, but earlier than Aristovo. The number of gaps (ghost ranges) in the rearrangements generated is calculated dynamically, parallel to the generation of each sequence. The given number of sequences with the minimum number of gaps is accumulated in a dynamically sorted list, which, as the calculations are completed, is saved in an MS Excel file.

The above-mentioned condition of succession (fixation of the sequence of the most reliably dated assemblages) turned out to be necessary because available calculating power of the computer appeared insufficient for processing more than a trillion rearrangements needed for our 15 assemblages (the factorial 15! = 1307674368000). To overcome this difficulty, several ways of reducing the number of rearrangements to an acceptable level have been tested. The more radical among them was fixation of the sequence of several most reliably dated assemblages, in this case, Kargala → Isady → Vyazniki → Nedubrovo (Tables 5, 6). Another way was reducing the number of assemblages analyzed to 13, which decreases the number of required rearrangements to six billion (13! = 6227020800). The reduction was performed by either excluding relatively poor assemblages of Suriekova and Sokolova (Tables 7–10) or combining two pairs of assemblages (Bor-Tologoi with Karaungir and Babii Kamen' with Tunguska; Tables 11–14).

The latter way allows reducing the amount of calculations to an acceptable level without sacrificing any materials, but it requires additional substantiation. Combining the assemblages of Tunguska and Babii Kamen' is justified by the fact that both assemblages are intertrappean and, consequently, approximately contemporaneous, although they are divided by a considerable distance (see above). The possibility to combine the even more remote assemblages of Karaungir and Bor-Tologoi was only revealed in the course of this study; in all variants of optimizing the sequence, the two assemblages were positioned almost invariably next to each other (Tables 5, 9) and, in Karaungir, the first or last appearances of families almost have not been recorded (Tables 4, 6, 8, 10). In other words, the proximity of these assemblages is obvious.

Another important parameter, the *renewal measure* (ratio of the numbers of the first or last appearances of families in each assemblage), which shows the direction of changes in assemblages, its enrichment or depletion, certainly depends on the position occupied by particular assemblage in the general sequence (cf. Tables 3, 4, and 6; 7, 8, and 10; 11, 12, and 14). It cannot be used for ordination of assemblages, but,

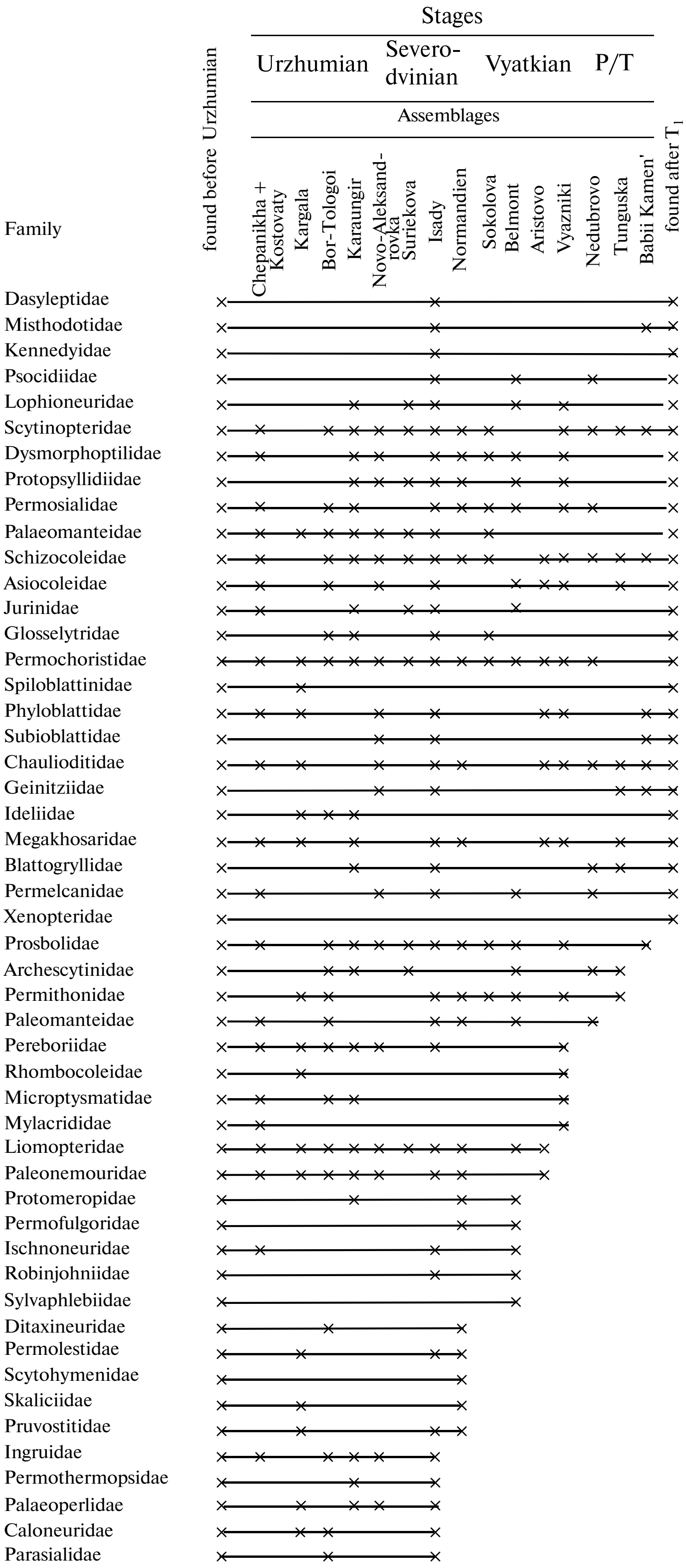


Fig. 92. Distribution of insect families over the stratigraphic range under study (preferred sequence of assemblages, as in Table 4). For sources on each record, see Table 2.

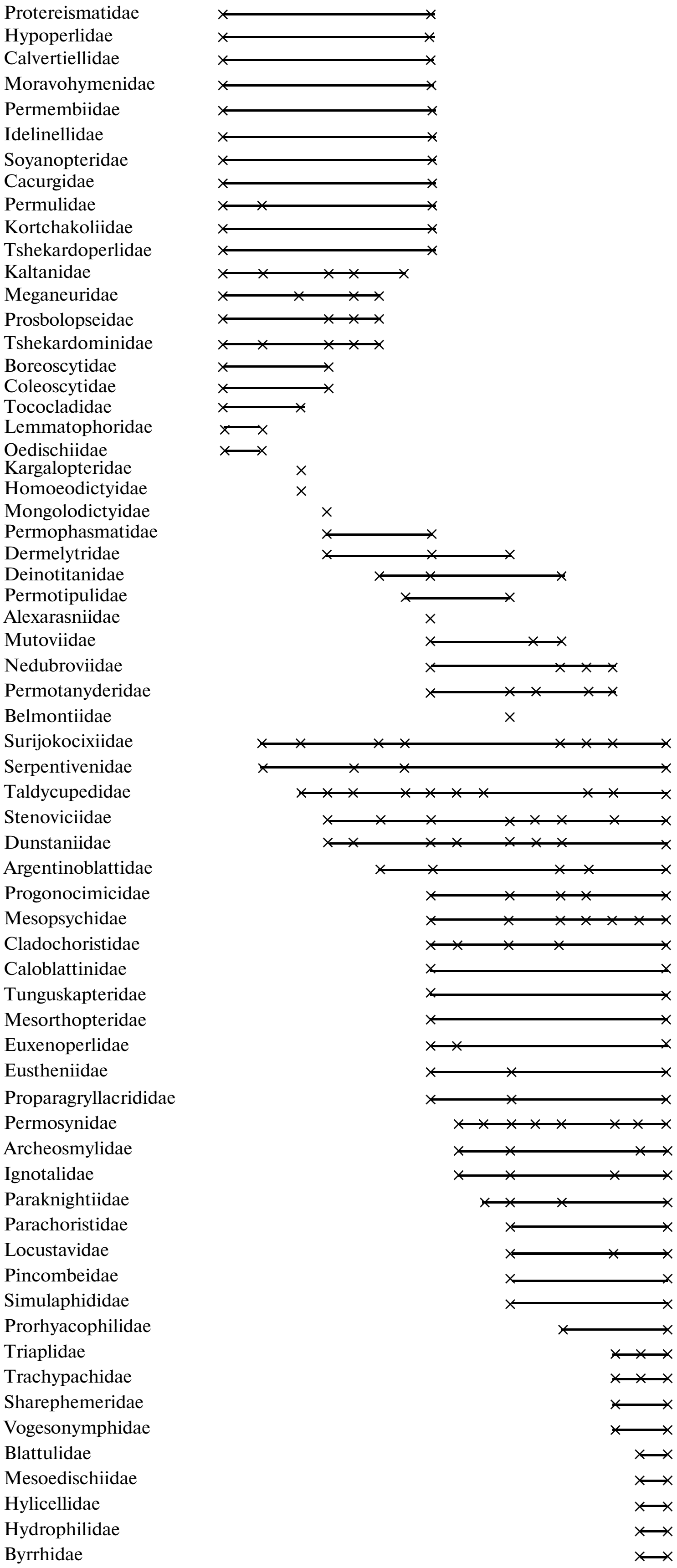

Protereismatidae
Hypoperlidae
Calvertiellidae
Moravohymenidae
Permembiidae
Idelinellidae
Soyanopteridae
Cacurgidae
Permulidae
Kortchakoliidae
Tshekardoperlidae
Kaltanidae
Meganeuridae
Prosbolopseidae
Tshekardominidae
Boreoscytidae
Coleoscytidae
Tococladidae
Lemmatophoridae
Oedischiidae
Kargalopteridae
Homoeodictyidae
Mongolodictyidae
Permophasmatidae
Dermelytridae
Deinotitanidae
Permotipulidae
Alexarasniidae
Mutoviidae
Nedubroviidae
Permotanyderidae
Belmontiidae
Surijokocixiidae
Serpentivenidae
Taldycupedidae
Stenoviciidae
Dunstaniidae
Argentinoblattidae
Progonocimicidae
Mesopsychidae
Cladochoristidae
Caloblattinidae
Tunguskapteridae
Mesorthopteridae
Euxenoperlidae
Eustheniidae
Proparagryllacrididae
Permosynidae
Archeosmylidae
Ignotalidae
Paraknightiidae
Parachoristidae
Locustavidae
Pincombeidae
Simulaphididae
Prorhyacophilidae
Triaplidae
Trachypachidae
Sharephemeridae
Vogesonymphidae
Blattulidae
Mesoedischiidae
Hylicellidae
Hydrophilidae
Byrrhidae

Fig. 92. (Contd.)

Table 6. Complete set of assemblages with four fixed sequences with the minimum number of ghost ranges (590: Table 8, line 2). For designations, see Table 5

Assemblage	Chepanikha + Kostovaty	Kargala	Karaungir	Bor-Tologoi	Isady	Novo-Aleksandrovka	Normandien	Vyazniki	Aristovo	Belmont	Suriekova	Nedubrovo	Sokolova	Tunguska	Babii Kamen'
Total number of specimens	400	300	550	900	3500	300	250	350	250	2000	670	200	570	600	140
$\ln_{total}$	6.0	5.7	6.3	6.8	8.2	5.7	5.5	5.9	5.5	7.6	6.5	5.3	6.3	6.4	4.9
Total number of families	29	23	31	32	69	26	30	30	13	37	18	18	13	22	18
Families/$\ln_{total}$	4.7	4.0	4.9	4.4	8.6	4.6	5.5	5.2	2.5	4.9	2.8	3.6	2.1	3.1	3.7
Number of first appearances	2	3	0	3	14	0	3	2	0	6	0	0	0	4	5
First/$\ln_{total}$	0.3	0.5	0	0.4	1.7	0	0.5	0.3	0	0.8	0	0	0	0.6	1.0
Number of last appearances	2	3	0	3	19	6	5	4	2	7	3	1	1	4	1
Last/$\ln_{total}$	0.3	0.5	0	0.4	2.3	1.0	0.9	0.7	0.4	0.9	0.5	0.2	0.2	0.6	0.2
Number of transitional	12	7	13	8	22	12	9	11	6	9	8	9	7	7	7
Number of transitional/$\ln_{total}$	2.0	1.2	2.1	1.2	2.7	2.1	1.6	1.9	1.1	1.2	1.2	1.7	1.1	1.1	1.4
Number of Paleozoic	14	12	15	18	26	10	14	6	2	11	6	2	3	2	1
Number of Paleozoic/$\ln_{total}$	2.3	2.1	2.4	2.6	3.2	1.7	2.5	1.0	0.4	1.4	0.9	0.4	0.5	0.3	0.2
Number of post-Paleozoic	2	2	3	3	13	3	7	10	3	13	3	5	3	11	10
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	0.4	1.6	0.5	1.3	1.7	0.5	1.7	0.5	0.9	0.5	1.7	2.0
Number of endemics	0	2	0	3	7	1	0	3	2	4	1	2	0	2	0
Endemics/$\ln_{total}$	0	0.3	0	0.4	0.8	0.2	0	0.5	0.4	0.5	0.1	0.4	0	0.3	0
First/last	1	1	/0	1	0.7	0	0.6	0.5	0	0.9	0	0	0	1	5.0
Pz/pPz	7.0	6.0	5.0	6.0	2.0	3.3	2.0	0.6	0.7	0.8	2.0	0.4	1.0	0.2	0.1
Turnover	0.7	1.0	0	0.9	4.0	1.0	1.5	1.0	0.4	1.7	0.5	0.2	0.2	1.2	1.2

Table 7. First reduced initial sequence (without Suriekova and Sokolova; sum of gaps 533). For designations, see Table 3

Assemblage	Kargala	Chepanikha + Kostovaty	Novo-Aleksandrovka	Isady	Bor-Tologoi	Karaungir	Belmont	Normandien	Aristovo	Vyazniki	Babii Kamen	'Tunguska	Nedubrovo
Total number of specimens	300	400	300	3500	900	550	2000	250	250	350	140	600	200
$\ln_{total}$	5.7	6.0	5.7	8.2	6.8	6.3	7.6	5.5	5.5	5.9	4.9	6.4	5.3
Total number of families	23	29	26	69	32	31	37	30	13	30	18	22	18
Families/$\ln_{total}$	4.0	4.7	4.6	8.6	4.4	4.9	4.9	5.5	2.5	5.2	3.7	3.1	3.6
Number of first appearances	4	1	3	16	1	0	9	1	0	1	7	2	0
first/$\ln_{total}$	0.7	0.2	0.5	1.9	0.1	0	1.2	0.2	0	0.2	1.4	0.3	0
Number of last appearances	3	2	0	12	6	7	6	7	3	6	1	1	4
last/$\ln_{total}$	0.5	0.3	0	1.5	0.9	1.1	0.8	1.3	0.5	1.0	0.2	0.2	0.7
Number of transitional	7	12	12	22	8	13	9	9	6	11	7	7	9
Number of transitional/$\ln_{total}$	1.2	2.0	2.1	2.7	1.2	2.1	1.2	1.6	1.1	1.9	1.4	1.1	1.7
Number of Paleozoic	12	14	10	26	18	15	11	14	2	6	1	2	2
Number of Paleozoic/$\ln_{total}$	2.1	2.3	1.7	3.2	2.6	2.4	1.4	2.5	0.4	1.0	0.2	0.3	0.4
Number of post-Paleozoic	2	2	3	13	3	3	13	7	3	10	10	11	5
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	1.6	0.4	0.5	1.7	1.3	0.5	1.7	2.0	1.7	0.9
Number of endemics	2	0	1	7	3	0	4	0	2	3	0	2	2
Endemics/$\ln_{total}$	0.3	0	0.2	0.8	0.4	0	0.5	0	0.4	0.5	0	0.3	0.4
First/last	1.3	0.5	/0	1.3	0.2	0	1.3	0.1	0	0.2	7.0	2.0	0
Pz/pPz	6.0	7.0	3.3	2.0	6.0	5.0	0.8	2.0	0.7	0.6	0.1	0.2	0.4
Turnover	1.2	0.5	0.5	3.4	1.0	1.1	2.0	1.5	0.5	1.2	1.6	0.5	0.7

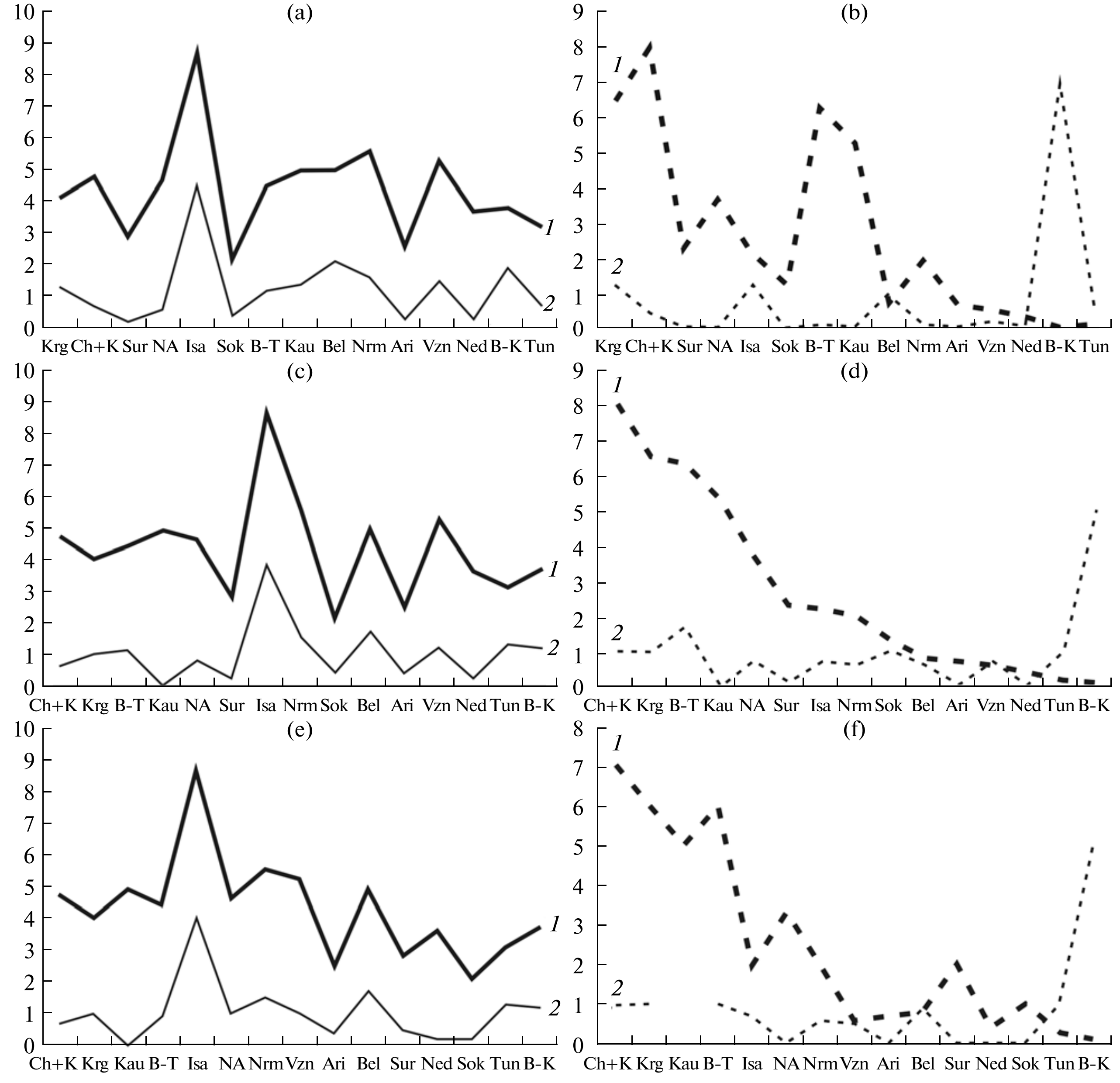


Fig. 93. Dynamics of insect families over the stratigraphic range under study, complete set of assemblages: (a, b) initial sequence (Table 3): (a) normalized number of families (*1*) and turnover measure (*2*); (b) faunal pattern index Pz/pPz (*1*) and renewal measure (ratio of first to last appearances) (*2*); (c, d) sequence optimized by the faunal pattern (Pz/pPz) (Table 4): (c) normalized number of families (*1*) and turnover measure (*2*); (d) faunal pattern index Pz/pPz (*1*) and renewal measure (*2*); (e, f) sequence of assemblages optimized by minimum number of gaps, the sequence Kargala–Isady–Vyazniki–Nedubrovo is fixed (Table 6): (e) normalized number of families (*1*) and turnover measure (*2*); (f) faunal pattern index Pz/pPz (*1*) and renewal measure (2). Designation of assemblages: (Ari) Aristovo, Vologda Region; (B-K) Babii Kamen'; (B-T) Bor-Tologoi, Mongolia; (Bel) Belmont, Australia; (Ch + K) Chepanikha + Kostovaty (Udmurtia); (Isa) Isady, Vologda Region; (Kau) Karaungir, western Kazakhstan; (Krg) Kargala (Orenburg Region); (N-A) Novo-Aleksandrovka, Orenburg Region; (Ned) Nedubrovo; (Nrm) Normandien, South Africa; (Sok) Sokolova II, Kemerovo Region; (Sur*)* Suriekovo, Kemerovo Region; (Tun) intertrappean deposits of the Tunguska Basin; (Vzn) Vyazniki (Balymotikha and Sokovka, Vladimir Region) (for more detail, see the text).

when the ordination is established, this measure becomes an important analytical tool.

The above-said is also true of the last tool used. The *faunal turnover measure* is calculated as the sum of the normalized numbers of first and last appearances and shows the intensity of changes regardless of their direction. All above methods and approaches are questioned by Labandeira (2005), who refers to the Signor–Lipps effect (Signor and Lipps, 1982), which is responsible for "that the last occurrences of variably preserved or moderately sampled fossil taxa at a major extinction will be recorded in a stepwise fashion back

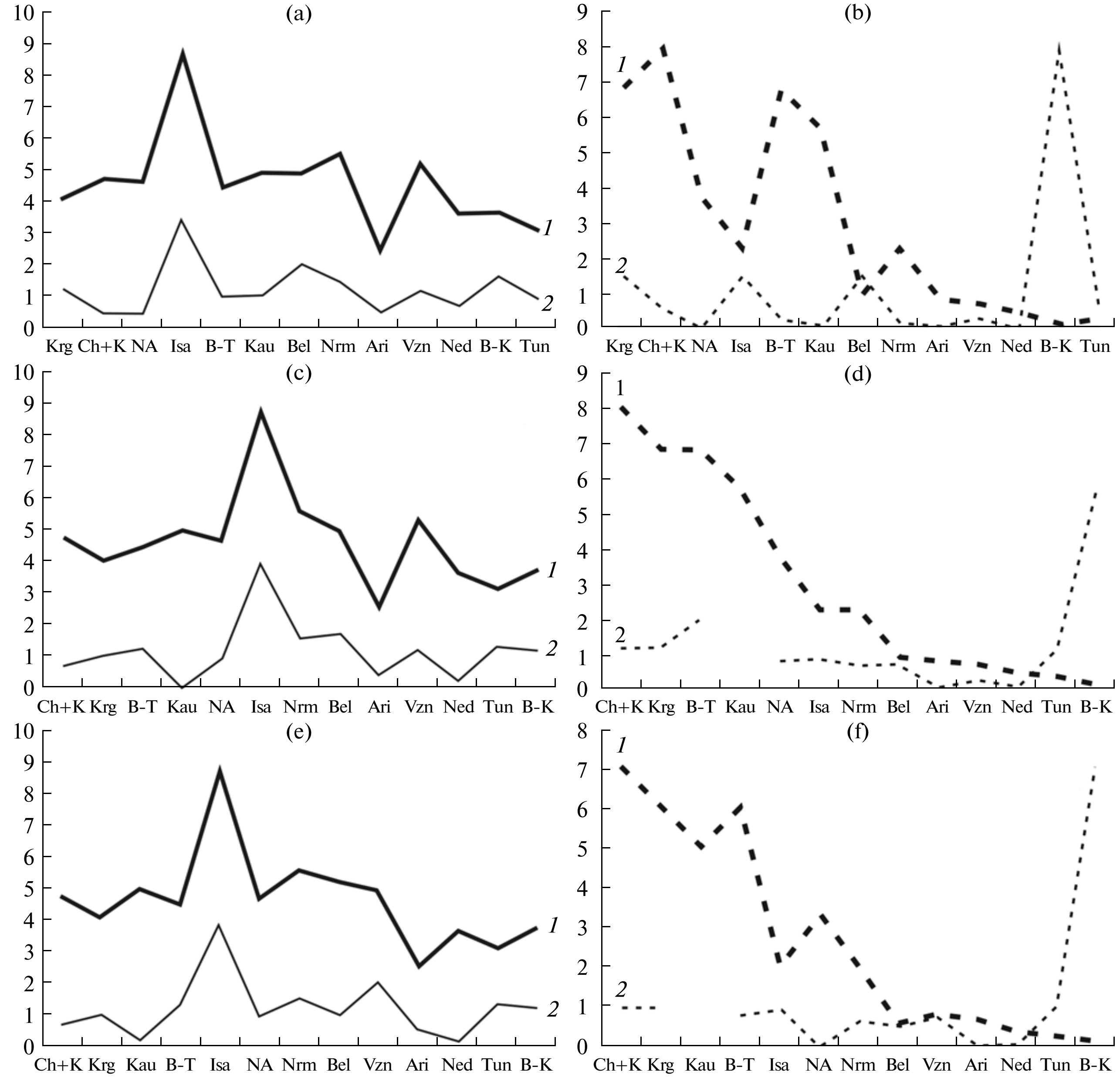


Fig. 94. Dynamics of insect families, first reduced sequence (Suriekova and Sokolova are excluded): (a, b) initial sequence (Table 7): (a) normalized number of families (*1*) and turnover measure (*2*); (b) faunal pattern index Pz/pPz (*1*) and renewal measure (ratio of first to last appearances) (*2*); (c, d) sequence normalized by faunal pattern Pz/pPz (Table 8): (c) normalized number of families (*1*) and turnover measure (*2*); (d) Pz/pPz (*1*) and renewal measure (*2*); (e, f) sequence of assemblages optimized by minimum number of gaps (Table 10): (e) normalized number of families (*1*) and turnover measure (*2*); (f) Pz/pPz (*1*) and renewal measure (*2*). For designations, see Fig. 93.

onto immediately earlier time units from the actual event. Thus, there is a stair-stepped pattern to last fossil occurrences that segregates taxa with a poorer fossil record from those with a better record. This pattern gives an impression that there are a series of earlier extinction events when in fact, they are an effect of a single, more massive extinction" (Labandeira 2005, p. 20). In other words, long stepwise (or gradual) decrease of diversity cannot falsify hypothesis of a single mass extinction event. This proposal cannot be accepted for several reasons.

First, when paleontologist speaks about extinction, the word is used highly metaphorically, for we have no tool to identify the real extinction time, as *Latimeria* Smith, 1939, *Grylloblatta* Walker, 1914, *Syntexis* Rohwer, 1915, and other living fossils witness irrefutably. We can only identify time when a taxon leaves the fossil record, that is, when the taxon went beyond a margin of the

Table 8. First reduced set of assemblages (without Suriekova and Sokolova), arranged according to Pz/pPz (number of gaps 503). For designations, see Table 3

Assemblage	Chepanikha + Kostovaty	Kargala	Bor-Tologoi	Karaungir	Novo-Aleksandrovka	Isady	Normandien	Belmont	Aristovo	Vyazniki	Nedubrovo	Tunguska	Babii Kamen'
Total number of specimens	400	300	900	550	300	3500	250	2000	250	350	200	600	140
$\ln_{total}$	6.0	5.7	6.8	6.3	5.7	8.2	5.5	7.6	5.5	5.9	5.3	6.4	4.9
Total number of families	29	23	32	31	26	69	30	37	13	30	18	22	18
Families/$\ln_{total}$	4.7	4.0	4.4	4.9	4.6	8.6	5.5	4.9	2.5	5.2	3.6	3.1	3.7
Number of first appearances	2	3	5	0	2	13	3	5	0	1	0	4	5
First/$\ln_{total}$	0.3	0.5	0.7	0	0.3	1.6	0.5	0.7	0	0.2	0	0.6	1.0
Number of last appearances	2	3	3	0	3	18	5	8	2	6	1	4	1
Last/$\ln_{total}$	0.3	0.5	0.4	0	0.5	2.2	0.9	1.0	0.4	1.0	0.2	0.6	0.2
Number of transitional	12	7	8	13	12	22	9	9	6	11	9	7	7
Number of transitional/$\ln_{total}$	2.0	1.2	1.2	2.1	2.1	2.7	1.6	1.2	1.1	1.9	1.7	1.1	1.4
Number of Paleozoic	14	12	18	15	10	26	14	11	2	6	2	2	1
Number of Paleozoic/$\ln_{total}$	2.3	2.1	2.6	2.4	1.7	3.2	2.5	1.4	0.4	1.0	0.4	0.3	0.2
number of post-Paleozoic	2	2	3	3	3	13	7	13	3	10	5	11	10
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.4	0.5	0.5	1.6	1.3	1.7	0.5	1.7	0.9	1.7	2.0
Number of endemics	0	2	3	0	1	7	0	4	2	3	2	2	0
Endemics/$\ln_{total}$	0	0.3	0.4	0	0.2	0.8	0	0.5	0.4	0.5	0.4	0.3	0
First/last	1	1	1.7	/0	0.7	0.7	0.6	0.6	0	0.2	0	1.0	5.0
Pz/pPz	7.0	6.0	6.0	5.0	3.3	2.0	2.0	0.8	0.7	0.6	0.4	0.2	0.1
Turnover	0.7	1.0	1.2	0	0.9	3.8	1.5	1.7	0.4	1.2	0.2	1.2	1.2

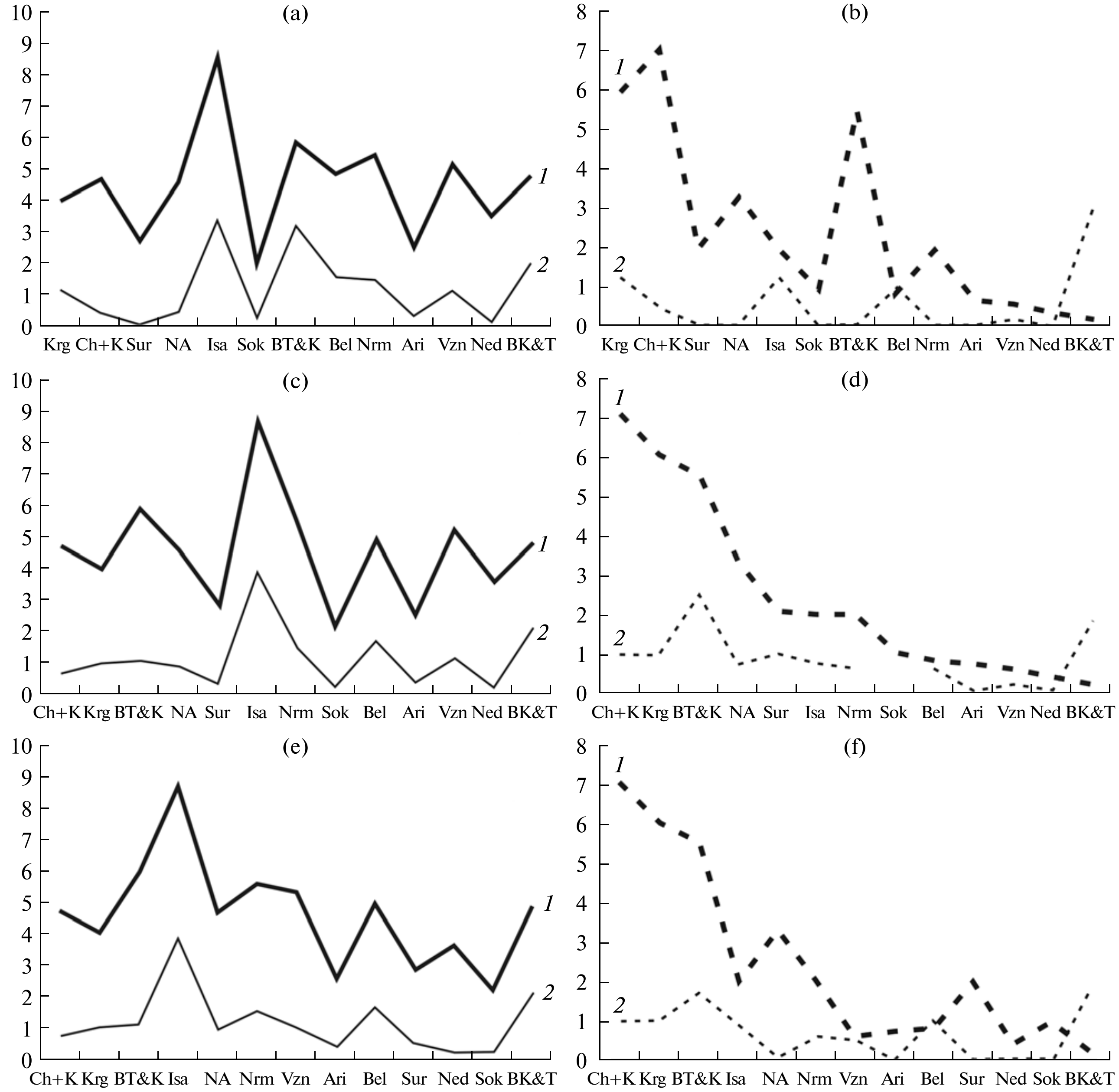


Fig. 95. Dynamics of insect families, second reduced sequence of assemblages (Bor-Tologoi is combined with Karaungir; Babii Kamen' is combined with Tunguska): (a, b) initial sequence (Table 11): (a) normalized number of families (*1*) and turnover measure (*2*); (b) faunal pattern index Pz/pPz (*1*) and renewal measure (ratio of first to last appearances) (*2*); (c, d) sequence normalized by faunal pattern Pz/pPz (Table 12): (c) normalized number of families (*1*) and turnover measure (*2*); (d) Pz/pPz (*1*) and renewal measure (*2*); (e, f) sequence of assemblages optimized by minimum number of gaps (Table 14): (e) normalized number of families (*1*) and turnover measure (*2*); (f) Pz/pPz (*1*) and renewal measure (*2*). Designations: (BT&K) combined assemblage of Bor-Tologoi and Karaungir; (BK&T) combined assemblage of Babii Kamen' and Tunguska; for other designations, see Fig. 93.

taphonomic window. In other words, when its taphonomic (recovery) potential went too much down due to loss of its abundancy and/or taphonomic diversity. This implies that the gradually (in wide sense, including stepwise) decreasing diversity is not an observational artifact (Signor–Lipps effect). Instead, it indicates a real process of decreasing taphonomic potential, which is traditionally (and correctly) interpreted as decreasing biodiversity.

The second reason to reject the Signor–Lipps effect as an explanation why slow and prolonged decrease in diversity could agree with the hypothesis of a single and geologically short mass extinction is in our results themselves. When studied at a more detailed stratigraphic scale then before, the insect diversity demonstrates neither gradual nor stepwise decrease toward the P/T boundary. Instead, after the end-Severodvinian peak, it varies cha-

Table 9. First reduced set of assemblages (without Suriekova and Sokolova): initial sequence and ten best sequences. For designations, see Table 5

533	Krga	Ch+Ko	N-Alek	Isad	B-T	Karau	Belm	Norm	Aris	Vyaz	Babiy	Tung	Ned
499	Ch+ K	Krga	Karau	B-T	Isad	N-Al	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy
500	Ch + K	Krga	Karau	B-T	Isad	N-Al	Norm	Vyaz	Aris	Belm	Ned	Tung	Babiy
501	Ch + K	Karau	Karg	B-T	Isad	N-Al	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy
502	Ch + K	Karau	B-To	Isad	N-Al	Krga	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy
503	Ch + K	Karau	B-To	Isad	N-Al	Krga	Norm	Vyaz	Aris	Belm	Ned	Tung	Babiy
504	Karau	Ch + K	Karg	B-To	Isad	N-Al	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy
505	Karau	Ch + K	B-T	Isad	N-Al	Krga	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy
506	Karau	Ch + K	B-T	Isad	N-Al	Krga	Norm	Vyaz	Aris	Belm	Ned	Tung	Babiy
507	Karau	B-T	Ch + K	Isad	N-Al	Krga	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy
508	Karau	B-T	Ch + K	Isad	Krga	N-Al	Norm	Vyaz	Belm	Aris	Ned	Tung	Babiy

otically within a rather narrow corridor, to give a new peak in the intertrappean time, that is, at the very moment of suggested biotic catastrophe (see Figs. 95c, 95d and text below).

3.1.3. Results

As follows from Table 3, the initial sequence is far from optimal by both criteria (Figs. 91, 93a, 93b). Optimizing it by the first criterion (Pz/pPz; Tables 4, Figs. 92, 93d, 93e) gives the sequence Chepanikha + Kostovaty—Kargala—Bor-Tologoi—Karaungir—Novo-Aleksandrovka—Suriekova—Isady—Normandien—Sokolova—Belmont—Aristovo—Vyazniki—Nedubrovo—intertrappean Tunguska—Babii Kamen' (cf. also Tables 8, 12, Figs. 94d, 94e, 95d, 95e). The differences from the initial sequence (Tables 3) are considerable, but they do not affect the sequence of well-dated assemblages (Kargala—Isady—Aristovo—Vyazniki—Nedubrovo). This gives evidence of the adequacy of the ordination method used. However, it should be taken into account that the faunal pattern criterion (Pz/pPz), at least in this case, has an obvious weak point: some values used are ratios of two small numbers (4/3 for Sokolova; 2/3 for Aristovo; 3/5 for Nedubrovo), so that the criterion is very vulnerable statistically. Interpretation of such data requires reasonable caution.

Optimization of the sequence of assemblages by the minimum sum of ghost ranges (Tables 6, 10, 14; Figs. 93e, 93f, 94e, 94f, 95e, 95f) gives rise to certain other problems. The differences between the best sequences by this criterion are minimum; the reliability of such differences is, therefore, low and, hence, the choice of a single best sequence is a nontrivial task. The solution we use for this problem is based on informal analysis of several (in this case, ten) best sequences and scrutiny of the trends revealed. It is shown that, among the complete set of assemblages (with four of them fixed; Table 5), the sequence Normandien—Vyazniki—Aristovo—Belmont—Suriekova—Nedubrovo—Sokolova—intertrappean Tunguska—Babii Kamen' is stably reproduced. In the first reduced set (Table 9), in all ten sequences, the segment including Normandien—Vyazniki—(Belmont—Aristovo)—Nedubrovo—Tunguska—Babii Kamen' remains stable (with the order of Belmont and Aristovo randomly alternating). The second reduced set (Table 13) yields almost the same stable unit, Aristovo—Belmont—Suriekova—Nedubrovo—Sokolova—intertrappean, which is preceded by randomly alternating Normandien and Vyazniki.

In the first half of the sequence, in all three variants, only the position of the Chepanikha—Kostovaty assemblage at the very beginning of the list is more or less stably reproduced. Subsequently, a certain order is not observed, although based on three or four upper lines, the complete set with four assemblages fixed (Table 5) is characterized by random alternation of Kargala, Karaungir, and Bor-Tologoi, stably followed by Isady and, then, by Novo-Aleksandrovka. A similar pattern is found in the first reduced set (Table 9), while the second reduced set (Table 13) includes a more definitive sequence of Chepanikha + Kostovaty—Kargala—(Bor-Tologoi + Karaungir)—Isady—Novo-Aleksandrovka. Comparison of these data with the sequence optimized by the faunal pattern criterion (Chepanikha + Kostovaty—Kargala—Bor-Tologoi—Karaungir—Novo-Aleksandrovka—Suriekova—Isady—Normandien—Sokolova—Belmont—Aristovo—Vyazniki—Nedubrovo—intertrappean Tunguska—Babii Kamen') shows a certain, but incomplete similarity. The position of Isady before or after Novo-Aleksandrovka apparently indicates the small difference in age between these localities, beyond the sensitivity of the method, if applied to insufficiently large material (as is the case of Novo-Aleksandrovka). A much stronger difference is found in the position of the Suriekova, Sokolova, and Vyazniki assemblages: ordination by minimum number of gaps results in the first two shifted far to the right (suggesting a younger age) and Vyazniki shifted to the left (older age) compared to the ordering by the faunal pattern (Pz/pPz). Vyazniki

Table 10. First reduced set of assemblages (without Suriekova and Sokolova) arranged based on the minimum number of gaps (Table 5, line 2: total number of gaps 499). For designations, see Table 3

Assemblage	Chepanikha + Kostovaty	Kargala	Karaungir	Bor-Tologoi	Isady	Novo-Aleksandrovka	Normandien	Vyazniki	Belmont	Aristovo	Nedubrovo	Tunguska	Babii Kamen'
Total number of specimens	400	300	550	900	3500	300	250	350	2000	250	200	600	140
$\ln_{total}$	6.0	5.7	6.3	6.8	8.2	5.7	5.5	5.9	7.6	5.5	5.3	6.4	4.9
Total number of families	29	23	31	32	69	26	30	30	37	13	18	22	18
Families/$\ln_{total}$	4.7	4.0	4.9	4.4	8.6	4.6	5.5	5.2	4.9	2.5	3.6	3.1	3.7
Number of first appearances	2	3	1	4	15	0	3	2	6	0	0	4	5
First/$\ln_{total}$	0.3	0.5	0.2	0.6	1.8	0	0.5	0.3	0.8	0	0	0.6	1.0
Number of last appearances	2	3	0	5	16	5	5	4	9	3	1	4	1
Last/$\ln_{total}$	0.3	0.5	0	0.7	1.9	0.9	0.9	0.7	1.2	0.5	0.2	0.6	0.2
Number of transitional	12	7	13	8	22	12	9	11	9	6	9	7	7
Number of transitional/$\ln_{total}$	2.0	1.2	2.1	1.2	2.7	2.1	1.6	1.9	1.2	1.1	1.7	1.1	1.4
Number of Paleozoic	14	12	15	18	26	10	14	6	11	2	2	2	1
Number of Paleozoic/$\ln_{total}$	2.3	2.1	2.4	2.6	3.2	1.7	2.5	1.0	1.4	0.4	0.4	0.3	0.2
Number of post-Paleozoic	2	2	3	3	13	3	7	10	13	3	5	11	10
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	0.4	1.6	0.5	1.3	1.7	1.7	0.5	0.9	1.7	2.0
Number of endemics	0	2	0	3	7	1	0	3	4	2	2	2	0
Endemics/$\ln_{total}$	0	0.3	0	0.4	0.8	0.2	0	0.5	0.5	0.4	0.4	0.3	0
First/last	1	1	/0	0.8	0.9	0	0.6	0.5	0.7	0	0	1	7.0
Pz/pPz	7.0	6.0	5.0	6.0	2.0	3.3	2.0	0.6	0.8	0.7	0.4	0.2	0.1
Turnover	0.7	1.0	0.2	1.3	3.8	0.9	1.5	1.0	2.0	0.5	0.2	0.2	1.2

Table 11. Second reduced set of assemblages (pairs Bor-Tologoi and Karaungir, Tunguska and Babii Kamen' are combined; total number of gaps 553). Intertrappean: Tunguska and Babii Kamen'; for designations, see Table 3

Assemblage	Kargala	Chepanikha + Kostovaty	Suriekovo	Novo-Aleksandrovka	Isady	Sokolova	Bor-Tologoi + Karaungir	Belmont	Normandien	Aristovo	Vyazniki	Intertrappean	Nedubrovo
Total number of specimens	300	400	670	300	3500	570	1450	2000	250	250	350	740	200
$\ln_{total}$	5.7	6.0	6.5	5.7	8.2	6.3	7.3	7.6	5.5	5.5	5.9	6.6	5.3
Total number of families	23	29	18	26	69	13	43	37	30	13	30	32	18
Families/$\ln_{total}$	4.0	4.7	2.8	4.6	8.6	2.1	5.9	4.9	5.5	2.5	5.2	4.8	3.6
Number of first appearances	4	1	1	3	16	2	1	6	1	0	1	9	0
First/$\ln_{total}$	0.7	0.3	0.1	0.5	1.6	0.3	0.1	0.8	0.2	0	0.2	1.4	0
Number of last appearances	3	2	0	0	12	0	23	14	7	2	8	3	4
Last/$\ln_{total}$	0.5	0.3	0	0	1.7	0	3.1	1.2	1.3	0.2	1.2	0.4	0.7
Number of transitional	7	12	8	12	22	7	14	9	9	6	11	10	9
Number of transitional/$\ln_{total}$	1.2	2.0	1.2	2.1	2.7	1.1	1.9	1.2	1.6	1.1	1.9	1.5	1.7
Number of Paleozoic	12	14	6	10	26	3	22	11	14	2	6	3	2
Number of Paleozoic/$\ln_{total}$	2.1	2.3	0.9	1.7	3.2	0.5	3.0	1.4	2.5	0.4	1.0	0.4	0.4
Number of post-Paleozoic	2	2	3	3	13	3	4	13	7	3	10	17	5
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	0.5	1.6	0.5	0.5	1.7	1.3	0.5	1.7	1.1	0.9
Number of endemics	2	0	1	1	7	0	3	4	0	2	3	2	2
Endemics/$\ln_{total}$	0.3	0	0.1	0.2	0.8	0	0.4	0.5	0	0.4	0.5	0.3	0.4
First/last	1.3	0.5	/0	/0	1.3	/0	~0	1.0	0.1	0	0.2	3.0	0
Pz/pPz	6.0	7.0	2.0	3.3	2.0	1.0	5.5	0.8	2.0	0.7	0.6	0.2	0.4
Turnover	1.2	0.5	0.1	0.5	3.4	0.3	3.3	1.6	1.5	0.4	1.2	1.8	0.7

Table 12. Second reduced set of assemblages optimized based on Pz/pPz (number of gaps 514). For designations, see Tables 3 and 11

Assemblage	Chepanikha + Kostovaty	Kargala	Bor-Tologoi + Karaungir	Novo-Aleksandrovka	Suriekovo	Isady	Normandien	Sokolova	Belmont	Aristovo	Vyazniki	Nedubrovo	intertrappean
Total number of specimens	400	300	1450	300	670	3500	250	570	2000	250	350	200	740
$\ln_{total}$	6.0	5.7	7.3	5.7	6.5	8.2	5.5	6.3	7.6	5.5	5.9	5.3	6.6
Total number of families	29	23	43	26	18	69	30	13	37	13	30	18	32
Families/$\ln_{total}$	4.7	4.0	5.9	4.6	2.8	8.6	5.5	2.1	4.9	2.5	5.2	3.6	4.8
Number of first appearances	2	3	5	2	1	13	3	1	5	0	1	0	9
First/$\ln_{total}$	0.3	0.5	0.7	0.3	0.1	1.6	0.5	0.2	0.7	0	0.2	0	1.4
Number of last appearances	2	3	3	3	1	18	5	0	8	2	6	1	5
Last/$\ln_{total}$	0.3	0.5	0.4	0.5	0.1	2.2	0.9	0	1.0	0.4	1.0	0.2	0.8
Number of transitional	12	7	14	12	8	22	9	7	9	6	11	9	10
Number of transitional/$\ln_{total}$	2.0	1.2	1.9	2.1	1.2	2.7	1.6	1.1	1.2	1.1	1.9	1.7	1.5
Number of Paleozoic	14	12	22	10	6	26	14	3	11	2	6	2	3
Number of Paleozoic/$\ln_{total}$	2.3	2.1	3.0	1.7	0.9	3.2	2.5	0.5	1.4	0.4	1.0	0.4	0.4
Number of post-Paleozoic	2	2	4	3	3	13	7	3	13	3	10	5	17
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	0.5	0.5	1.6	1.3	0.5	1.7	0.5	1.7	0.9	1.1
Number of endemics	0	2	3	1	1	7	0	0	4	2	3	2	2
Endemics/$\ln_{total}$	0	0.3	0.4	0.2	0.1	0.8	0	0	0.5	0.4	0.5	0.4	0.3
First/last	1	1	2.5	0.7	1	0.7	0.6	/0	0.6	0	0.2	0	1.8
Pz/pPz	7.0	6.0	5.5	3.3	2.0	2.0	2.0	1.0	0.8	0.7	0.6	0.4	0.2
Turnover	0.7	1.0	1.1	0.9	0.3	3.8	1.5	0.23	1.7	0.4	1.2	0.2	2.1

Table 13. Second reduced set of assemblages: initial sequence and ten best sequences according to the number of gaps. Designations: (B-T&K) combined assemblage of Bor-Tologoi and Karaungir; (intertrap) intertrappean assemblages of Tunguska and Babii Kamen'; For other designations, see Table 5

553	Krga	Ch + K	Suri	N-Alek	Isad	Soko	B-T&K	Belm	Norm	Aris	Vyaz	intertrap	Nedu
493	Ch + K	Krga	B-T&K	Isad	N-Alek	Norm	Vyaz	Aris	Belm	Suri	Nedu	Soko	intertrap
494	Ch + K	Krga	B-T&K	Isad	N-Alek	Norm	Aris	Vyaz	Belm	Suri	Nedu	Soko	intertrap
495	Ch + K	Krga	B-T&K	Isad	N-Alek	Vyaz	Norm	Aris	Belm	Suri	Nedu	Soko	intertrap
496	Ch + K	B-T&K	Isad	N-Alek	Krga	Norm	Vyaz	Aris	Belm	Suri	Nedu	Soko	intertrap
498	Ch + K	B-T&K	Isad	N-Alek	Krga	Vyaz	Norm	Aris	Belm	Suri	Nedu	Soko	intertrap
500	B-T&K	Ch + K	Isad	N-Alek	Krga	Norm	Vyaz	Aris	Belm	Suri	Nedu	Soko	intertrap
502	B-T&K	Isad	Ch + K	N-Alek	Krga	Norm	Vyaz	Aris	Belm	Suri	Nedu	Soko	intertrap
504	B-T&K	Isad	N-Alek	Ch + K	Krga	Norm	Vyaz	Aris	Belm	Suri	Nedu	Soko	intertrap
506	B-T&K	Isad	N-Alek	Ch + K	Krga	Vyaz	Norm	Aris	Belm	Suri	Nedu	Soko	intertrap
508	B-T&K	Isad	N-Alek	Ch + K	Krga	Aris	Norm	Vyaz	Belm	Suri	Nedu	Soko	intertrap

appears older than Belmont, Suriekova is younger than Belmont, and Sokolova is younger than Nedubrovo. This result is in conflict with available geological data (see above in this section and Chapter 1.3 for Vyazniki); therefore, it should not be taken for a plausible model. Possible causes of this contradiction are discussed below, but, in any case, the data on the dynamics of the faunal pattern (Pz/pPz) should be preferred here.

Among other results, we should primarily pay attention to the parallel (to a first approximation) trend of changes in local diversity (normalized number of families per assemblage) and faunal turnover measure (Figs. 93a, 94a, 95a). This predictable result is evidence of the absence or scarcity of anomalous processes, in which a poor assemblage shows a relatively higher number of the first and/or last appearances of families and vice versa. It is not improbable that, in this case, anomalous assemblages come from Karaungir and, less certainly, Kargala; these assemblages stably (i.e., in different versions of calculations) demonstrate rates of renewal lower and higher than expected, respectively. The analysis of causes of these possible anomalies should be postponed until a greater amount of similar data is accumulated.

3.1.4. Discussion

Turning to the discussion of results, we should primarily mark the difficulties of correlation of the assemblages studied. More or less reliable stratigraphic data (see Chapter 1 and this section above) only give evidence that the Chepanikha, Kostovaty, and Kargala localities were formed not later than the Urzhumian, Middle Permian; Isady is near the upper boundary of the Severodvinian; Vyazniki is near the upper boundary of the Upper Vyatkian; Aristovo is more or less immediately followed by Vyazniki; and the Nedubrovo and intertrappean assemblages are not earlier than the nearest neighborhood of the Permian–Triassic boundary. Therefore, it is not always possible to correlate events revealed in the history of insects during the Urzhumian–Lower Triassic period with the stratigraphic units of the General and International scales. Nevertheless, our data allow specifying this correlation.

As shown above, the optimizing methods used in the present study reveal two alternative sequences:

(1) Chepanikha + Kostovaty–Kargala–Bor-Tologoi–Karaungir–Novo-Aleksandrovka–Suriekova–Isady–Normandien–Sokolova–Belmont–Aristovo–Vyazniki–Nedubrovo–intertrappean Tunguska–Babii Kamen’ (by the ratio of families considered Paleozoic and post-Paleozoic);

(2) (Chepanikha + Kostovaty)–Kargala–(Karaungir + Bor-Tologoi)–Isady–Novo-Aleksandrovka–Normandien–Vyazniki–(Belmont + Aristovo)–Suriekova–Nedubrovo–Sokolova–Tunguska–Babii Kamen’ (by minimum ghost ranges).

Sequence (1), on the whole, complies well with stratigraphic data and looks optimal. Its only somewhat unexpected component is the position of the Nedubrovo assemblage below the intertrappean assemblages of Tunguska and Babii Kamen’; however, the stratigraphic argumentation in favor of the opposite order is not very strong (see above in the section *Materials*). Since both of our criteria, the faunal pattern (Pz/pPz) and minimum of ghost ranges, unanimously suggest a lower position for Nedubrovo, we are compelled to rest on this conclusion. Sequence (2), as noted in the section *Results*, is more contradictory. The positions of Vyazniki below and Suriekova above Belmont and Aristovo and Sokolova above Nedubrovo contradict well-founded stratigraphic data (see above in this chapter and Chapter 3.1) and cannot be accepted. However, the causes of these contradictions deserve attention and analysis, since they are important for understanding the specifics of the methods and can contribute to the recognition of the trends not revealed by other parameters. The younger age (shift towards the end of the sequence) for small assemblages of Sokolova and Suriekova, the number of families in

Table 14. Second reduced set of assemblages optimized based on the total number of gaps (Table 12, second line; total number of gaps 493). For designations, see Tables 3 and 11

Assemblage	Chepanikha + Kostovaty	Kargala	Bor-Tologoi + Karaungir	Isady	Novo-Aleksandrovka	Normandien	Vyazniki	Aristovo	Belmont	Suriekova	Nedubrovo	Sokolova	intertrappean
Total number of specimens	400	300	1450	3500	300	250	350	250	2000	670	200	570	740
$\ln_{total}$	6.0	5.7	7.3	8.2	5.7	5.5	5.9	5.5	7.6	6.5	5.3	6.3	6.6
Total number of families	29	23	43	69	26	30	30	13	37	18	18	13	32
Families/$\ln_{total}$	4.7	4.0	5.9	8.6	4.6	5.5	5.2	2.5	4.9	2.8	3.6	2.1	4.8
Number of first appearances	2	3	5	15	0	3	2	0	6	0	0	0	9
First/$\ln_{total}$	0.3	0.5	0.7	1.8	0	0.5	0.3	0	0.8	0	0	0	1.4
Number of last appearances	2	3	3	16	5	5	4	2	6	3	1	1	5
Last/$\ln_{total}$	0.3	0.5	0.3	1.9	0.9	0.9	0.7	0.4	0.8	0.5	0.2	0.2	0.8
Number of transitional	12	7	14	22	12	9	11	6	9	8	9	7	10
Number of transitional/$\ln_{total}$	2.0	1.2	1.9	2.7	2.1	1.6	1.9	1.1	1.2	1.2	1.7	1.1	1.5
Number of Paleozoic	14	12	22	26	10	14	6	2	11	6	2	3	3
Number of Paleozoic/$\ln_{total}$	2.3	2.1	3.0	3.2	1.7	2.5	1.0	0.4	1.4	0.9	0.4	0.5	0.4
Number of post-Paleozoic	2	2	4	13	3	7	10	3	13	3	5	3	17
Post-Paleozoic/$\ln_{total}$	0.3	0.3	0.5	1.6	0.5	1.3	1.7	0.5	1.7	0.5	0.9	0.5	1.1
Number of endemics	0	2	3	7	1	0	3	2	4	1	2	0	2
Endemics/$\ln_{total}$	0	0.3	0.4	0.8	0.2	0	0.5	0.4	0.5	0.1	0.4	0	0.3
First/last	1	1	1.7	0.9	0	0.6	0.5	0	1	0	0	0	1.8
Pz/pPz	7.0	6.0	5.5	2.0	3.3	2.0	0.6	0.7	0.8	2.0	0.4	1.0	0.2
Turnover	0.7	1.0	1.1	3.8	0.9	1.5	1.0	0.4	1.6	0.5	0.2	0.2	2.1

which is 13 and 18, respectively, may be a mathematical artifact. Certainly, the entomofauna of the terminal Permian is depleted (see below), so that the number of gaps in the right wing of our distribution (Figs. 91, 92) is much greater than in its other parts. Small assemblages by definition display many gaps, and our method of minimizing ghost ranges (internal gaps within the temporal distribution of families) can automatically shift such assemblages to that end of the distribution where the number of such gaps is great. Consequently, the ordination of small assemblages by the method of ghost ranges can be especially unreliable. This is, of course, an entirely preliminary supposition, which requires testing. The case of the Vyazniki assemblage is different, but it is more convenient to discuss this paradox later.

For the time being, we accept sequence (1) in a generalized form as the final, combining assemblages most similar in available parameters:(3) (Chepanikha + Kostovaty)–Kargala–(Bor-Tologoi + Karaungir)–Novo-Aleksandrovka–(Suriekova–Isady–Normandien)–Sokolova–Belmont–Aristovo–Vyazniki–Nedubrovo–(intertrappean Tunguska + Babii Kamen’).

The reasons for combining Chapanikha with Kostovaty, Bor-Tologoi with Karaungir, and Tunguska with Babii Kamen’ are given above; Suriekova, Isady, and Normandien are combined based on their identical values of the faunal pattern index.

The results of our study allow making the following conclusions:

1. The change in the composition of insect families during the period studied was extremely uneven, with noncoincident moments of sharp changes in different parameters.

2. The faunal pattern of successive assemblages (Pz/pPz; Figs. 93d, 94d, 95d) changes smoothly; however, several stages of these changes are recognized. In early assemblages (Chepanikha–Novo-Aleksandrovka), ancient families (conditionally considered Paleozoic) strongly dominate. In Suriekovo, Isady, and Normandien, their dominance is distinct, but less pronounced. Starting with Sokolova, the proportion of ancient families smoothly decreases from parity to 1 : 5.

3. The direction of changes (the ratio of the number of the first and last appearances of families; Figs. 93d, 94d, 95d) changes more chaotically, but, on the whole, we can trace a very slow change from parity at the beginning to the disappearance of the first appearances to Nedubrovo (with a local peak in Bor-Tologoi) and a new peak of diversification in the intertrappean deposits of Siberia.

4. The intensity of changes, reflected in the turnover measure (Figs. 93c, 94c, 95c) seems chaotic, but, as mentioned above, it is mostly determined by the summarized diversity of respective assemblages. The chaotic changes in the last parameter are probably caused by the diversity of living conditions. Although the highest value of diversity (Isady) coincides with the largest size of collection and one of the lowest values (Aristovo) coincides with one of the smaller collections; in other cases, a distinct correlation between diversity and the size of collections is not observed. The four minimums observed (Suriekova, Sokolova, Aristovo, Nedubrovo) represent collections of different size (200 to 670 specimens), and medium values of diversity are found in collections ranging from 300 to 2000 specimens (other assemblages, except Isady). Therefore, it is hardly probable that the correlation between the rate of renewal and diversity of assemblages is caused by the direct influence of the extent of knowledge (number of specimens collected) and, hence, the insufficiency of diversity normalization by the logarithm of collection size (see the section *Materials*). The hypothesis of the influence of local environmental factors seems more feasible in many aspects, although other factors should also be looked for to gain a better understanding of the almost twofold growth of the renewal rate found in Isady. These factors may include, for instance, the unevenness of temporal distribution of assemblages: if the time between Isady and the nearest preceding and succeeding assemblages is very long, all other things being equal, proportionally greater numbers of the first and last appearances could have accumulated over a longer time. However, the Isady assemblage does not differ from the others, for instance, from Suriekova and Normandien, in other parameters, which are also time-dependent, e.g., in the faunal pattern (Pz/pPz). Thus, at present, there is no reason to appeal to the time gap hypothesis.

5. The following boundaries proved to be most important: (1) before Isady: the end of a rapid fall of the proportion of ancient families and transition to unbalanced changes, with the prevalence of the last appearances of families; (2) beginning from Belmont (or the insufficiently known Sokolova): transition to a very gradual decrease in the proportion of ancient families, retaining a strongly negative balance of changes; (3) intertrappean time: return to strongly positive dynamics in the composition of assemblages. The recognition of Isady as a special stage based on the sharp intensification of faunal renewal is questionable. It is not improbable that, in this case, we deal with results of certain specific local or regional conditions, or uniquely favorable fossilization conditions, i.e., that this phenomenon is geographic or taphonomic rather than evolutionary.

It is noteworthy that combining in one sequence large amounts of data on Angaraland (including Subangaraland) and considerably more limited data on Gondwana (one assemblage from Australia and one from South Africa) did not result in difficulties in interpretation. The data on the Belmont and Normandien assemblages are neatly integrated into the sequence of the Angaraland assemblages, without distorting this sequence. It proved even easier to combine in one sequence assemblages of European Russia, southern and central Siberia, eastern Kazakhstan, and Mongolia. This result suggests a largely global character of changes in the entomofauna around the Permian–Triassic boundary and, thus, the acceptability of the approach used here.

Taking these reservations into account, we can formulate the following preliminary conclusions. At the beginning of the period studied, the dynamics of the insect fauna at the taxonomic level of families had a balanced character. The first and last appearances approximately counterbalanced each other (with the exception of a short-term peak at the level of Bor-Tologoi); ancient (conditionally considered Paleozoic) families dominated over young ones (conditionally considered post-Paleozoic), but the extent of their dominance rapidly decreased. Beginning from Novo-Aleksandrovka and Isady, the negative component of changes stably prevailed and the Paleozoic faunal pattern (dominance of ancient families) gradually leveled out. The intensity of changes, which sharply increased in the Isady time, subsequently decreased, but the evolutionary rather than geographic or taphonomic nature of the Isady peak requires confirmation. The negative character of faunal turnover sharply intensified at least at the level of Vyazniki, if not Aristovo. At the transitional Permian–Triassic phase (Tunguska, Babii Kamen'), the taxonomic dynamics, approximately retaining its former intensity, changed to sharply positive and the faunal pattern became definitely post-Paleozoic.

According to these results and taking into account available stratigraphic data, we can tentatively propose a distribution pattern of the insect assemblages under study over the stratigraphic units of the Middle (its upper part) and Upper Permian. Chepanikha, Kostovaty, Kargala, Bor-Tologoi, and Karaungir, which are characterized by the faunal pattern index from 5 to 7, can be preliminarily correlated with the Urzhumian Stage of the Middle Permian. Novo-Aleksandrovka, Suriekova, Isady, and Normandien (Pz/pPz = 2–3,3) are assigned to the Severodvinian Stage of the Upper Permian; Sokolova, Belmont, Aristovo, and Vyazniki are dated as the Vyatkian Stage (Pz/pPz = 0.6–1). The position of intertrappean assemblages (Tunguska and Babii Kamen', Pz/pPz = 0.1–0.2) in the transitional P/T range is generally accepted. The position of Nedubrovo remains uncertain; it probably belongs to the Vyatkian Stage, the more so as the dominance of the last appearances over first ones makes it similar to presumably Vyatkian assemblages. However, a number of features of the Nedubrovo fauna and flora were previously interpreted as supporting its correlation with the post-trappean or late trappean level (see above). Therefore, the solution of this question should be postponed.

Doubtlessly Early Triassic (post-trappean) insect faunas are known very poorly. They are undoubtedly impoverished, but it is not at all easy to interpret this fact. Indeed, in the transitional P/T range (beginning from Nedubrovo) and doubtless Lower Triassic, 40 insect families have been recorded, while in the preceding range (Sokolova–Vyazniki, presumably Vyatkian, Late Permian), 47 families have been recorded, and in the range before that (Novo-Aleksandrovka–Normandien, presumably Severodvinian, Late Permian), there are 87 families; in the presumably Urzhumian time (Chepanikha–Karaungir), 59 families have been recorded. However, if we take into account not only the directly recorded families, but also those that have been recorded before and after each particular range and, thus, also existed in this range, but have not been found, the ratio will be different: 64 families in the Early Triassic, 67 in the Vyatkian, 96 in the Severodvinian, and 80 in the Urzhumian. Thus, the known Early Triassic insect fauna is not disastrously depleted; almost the same level of impoverishment is found in the preceding Vyatkian fauna. A more profound impoverishment (almost by one-third) is only observed in comparison with the rich Severodvinian fauna. However, if we normalize the diversity of insects over the stages (see the section *Methods*), the differences will change. Normalized insect diversity, taking into account transitional families, is 10.4 in the Urzhumian, 11.3 in the Severodvinian, 8.3 in the Vyatkian, and 9.4 in the Early Triassic (including transitional assemblages). Thus, it is the Vyatkian fauna, rather than the Early Triassic one, that is the most depleted, but even this fauna is depleted only by one-third compared with the richest Severodvinian fauna.

Thus, in the history of insects, the Permian–Triassic crisis (the meaning of this term in the context of this study is discussed below) begins with the dominance of negative events over positive ones and is possibly accompanied by a sharp short-term peak of dynamics (Isady). Extinction of families continues to dominate until the end of the Vyatkian and, only at the Permian–Triassic boundary, the emergence of new families begins to prevail. The crisis manifests itself in an inhibition of taxonomic diversification rather than intensification of extinction, because a mass extinction of insects did not occur at this boundary. This is why the change in the faunal pattern lags behind and the fauna becomes clearly post-Paleozoic only in the Vyazniki time, immediately before the transitional P/T range.

We can try to compare the results of this study with the previously performed analyses of the Cretaceous biocoenotic crisis (Zherikhin, 1978; Dmitriev and Zherikhin, 1988; Rasnitsyn, 1988, 1989; Bugdaeva et al., 2006). The scope of those studies included a considerably wider range, covering the terminal Jurassic and entire Cretaceous, and revealed a characteristic stepwise development of the process. For instance, successive phases of the crisis were formulated: preparatory, paradoxical, drastic, and calming (Rasnitsyn, 1989). It was pointed out that the preparatory phase is characterized by a rapid decrease in the proportion of extinct families (in our case, these are ancient families conditionally considered Paleozoic); the paradoxical phase is characterized by the deceleration of diversification and archaization of the fauna (temporary increase in the proportion of extinct families). The drastic phase is distinguished by a rapid renewal of the fauna; and the calming phase is distinguished by a decrease in the rate of faunal renewal, reaching the background level, primarily through deceleration of extinction. It was noted that, during the calming phase, "extinction quickly ceases, and emergence continues, sometimes even intensifying. Obviously, the crisis resulted in the appearance of communities with much greater capacities than before" (Rasnitsyn, 1989, p. 39).

A comparison of the results of the present study with the conclusions drawn in studies of the Cretaceous crisis reveals certain, although incomplete, similarity. The preparatory phase of the crisis in the case in question probably corresponds to the Urzhumian, when the proportion of ancient families sharply decreased, but the balance of changes remained positive or neutral (Figs. 93–95). During the Severodvinian and Vyatkian time, the proportion of ancient families continued to decrease rapidly, but not so much because of the emergence of young families as because of the continuing extinction of ancient ones, since diversification was suppressed and the balance of changes remained negative; the fauna became depleted. This stage probably represents a strongly protracted paradoxical phase of the crisis. At the same time, archaization of the fauna, described for this phase in the Cretaceous crisis, is not explicitly pronounced here (as a temporary increase in the proportion of ancient families). However, the above-noted paradoxical behavior of the Vyazniki assemblage in the case of ordination by the minimum number of stratigraphic gaps, where this assemblage precedes earlier assemblages from Belmont and Aristovo, may be simply a different manifestation of the same archaization phenomenon; this supposition requires special testing. It will be recalled that the Vyazniki assemblage shows a distinct archaic character, in particular, in traces of interactions between insects and plants (Chapter 1.4).

The beginning of the drastic phase is probably represented by transitional Permian–Triassic assemblages, especially intertrappean, characterized by a strong dominance of positive processes over negative ones and, possibly, by a general activation of faunal renewal. However, testing of this hypothesis is a matter for future studies. The drastic phase of the crisis is represented in the material of the present study at best by its very beginning, and the calming phase is not represented at all, so that little can be said about it. In any event, it is apparent that an almost complete cessation of extinction of families, as in the Paleogene, did not take place in the Mesozoic. However, a rapid growth of insect diversity, described for the Late Cretaceous and post-Cretaceous situation, is also clearly pronounced after the Permian crisis. According to Dmitriev (Dmitriev and Ponomarenko, 2002), the curve of insect families shows a slow growth in the Paleozoic, terminating in a small decrease in the latter half of the Permian and at the beginning of the Triassic and, then, from the Middle Triassic to Recent, stable rapid growth with a barely discernible decrease in its rate from the terminal Jurassic to terminal Cretaceous (Dmitriev and Ponomarenko, 2002, text-fig. 478b).

Thus, the events around the Permian–Triassic boundary, reflected in the composition of successive assemblages of insect families, had a rather complex pattern, resembling to some extent that of the polyphase Cretaceous biocoenotic crisis. By analogy, the Permian–Triassic biocoenotic crisis can also be recognized; however, the crisis character of the phenomenon is manifested in this case to an even greater extent than in the Cretaceous in the transformation of the community structure rather than negative processes, such as mass extinction. The new biocoenotic structure which emerged after the transformation proved to have such a high capacity that it gave rise to a rapid and almost uninterrupted growth of taxonomic diversity of insects during the entire Meso–Cenozoic, only with a Cretaceous decrease barely noticeable on this scale. Since the above-described pattern of the taxonomic dynamics of insects at the family level closely matches that of marine organisms within the range from the Carboniferous to Recent (with the major difference that extinctions in marine ecosystems around the Permian–Triassic and Cretaceous–Paleogene boundaries were rather strong: Alekseev et al., 2001, text-fig. 6), it is proposed that the reorganization of communities was an important, or even the most important, aspect and result of these and many other crises in the development of the biosphere.

Another conclusion, not so large-scale, but also deserving attention, is that a few more or less thoroughly examined insect assemblages outside Angaraland (from the African and Australian parts of Gondwana) are naturally integrated into the processes revealed in Angaraland, suggesting a considerable level of unity in the entomofauna of that time and a global character of the processes and events described. However, since the processes reconstructed based on fossil insects and marine animals prove to be similar (see above), there is no surprise that the processes in entomofaunas of Angaraland and Gondwana are also similar.

3.1.5. Conclusions

The results obtained by the group of paleoentomologists of PIN and their collaborators and generalized here display a relatively diverse insect fauna from localities of the terminal Permian and basal Triassic (Urzhumian to Olenekian). A total of 25 orders and 115 families of insects have been recorded; one family, 27 genera, and 117 species are newly described. Three orders (Caloneurida, Dictyoneurida, and Mischopterida) and nine families are recorded for the first time in the Late Permian. Fifteen more or less representative successive insect assemblages have been revealed (13 from Angaraland and two from Gondwana). Comparison of the composition of families in these assemblages has confirmed the absence of catastrophic extinction of insects at the boundary between the Late Permian and Triassic; a depletion took place during the Vyatkian, but it was not catastrophic during this age nor at the end of it. The Vyatkian decrease in diversity was caused mostly by deceleration of diversification rather than by actual extinction. The depletion of Vyatkian and Early Triassic assemblages was neither catastrophic nor global. In the Early Triassic, including the transitional period, only 46% of families recorded in the preceding Severodvinian Time have been found; in the Vyatkian Time, there were 54% of such families. However, taking into account transitional families not recorded in particular periods, Vyatkian and Early Triassic assemblages contain 70 and 67% of Severodvinian families, respectively. In the Vyatkian and Early Triassic, the probability for insects to fall in the burial probably in general decreased due to a decrease in ranges (survival in refugia), unfavorable changes in fossilization conditions, or some other presently uncertain reasons.

The pattern of changes revealed in the present study displays certain, although incomplete, similarity to the stages (phases) of the Cretaceous biocoenotic crisis; the difference of the Permian–Triassic crisis is the even smaller, compared to the Cretaceous, contribution of negative processes (extinction). The reorganization of the biocoenotic structure towards unlimited growth of its capacity becomes a factor of primary importance, as in the Cretaceous.

Some other aspects and features of insect evolution near the P/T boundary are discussed in other publcations based on the present study (Rasnitsyn, 2012; Rasnitsyn et al., 2013).

The methods developed in the course of this study for ordination of fossil assemblages of insufficiently clear stratigraphic position proved quite efficient and deserve further testing with the use of other groups and stratigraphic levels and, probably (in the case of ordination by the sum of ghost ranges), even in fields beyond paleontology. Using these methods with paleoentomological materials is quite promising for fine correlation of deposits on both the regional and global scale.

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