

New Blattinopsidae (Insecta: Blattinopsida) in the Permian of the Pechora Basin (Komi Republic, Russia) in the Context of Landscape and Vegetation Evolution

D. S. Aristov^{a, b, *}, A. P. Rasnitsyn^{a, c, **}, and S. V. Naugolnykh^{d, ***}

^a Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia

^b Cherepovets State University, Cherepovets, 162602 Russia

^c Natural History Museum, London, London, SW7 5BD UK

^d Geological Institute, Russian Academy of Sciences, Moscow, 119017 Russia

*e-mail: danil_aristov@mail.ru

**e-mail: alex.rasnitsyn@gmail.com

***e-mail: naugolnykh@list.ru

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Abstract—Permian Blattinopsida in the Vorkuta Group of the Pechora Basin (Komi Republic, northern Russia) are reviewed. *Glaphyrophlebia komia* sp. nov., *G. vorkutensis* sp. nov., and *G. borea* sp. nov. are described from the Inta Formation. The taxonomic composition of plants in the Kungurian-Ufimian interval is analyzed for the Pechora Basin in comparison with that in Cisuralia.

Keywords: Insecta, Blattinopsida, Blattinopsidae, Lower Permian, Middle Permian, Russia, paleobotany

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INTRODUCTION

New phytophagous blattinopsid insects (Rasnitsyn, 1980b) are described in this paper and the flora from the Vorkuta Group in the Pechora Basin (hereinafter, the term Vorkuta is sometimes used for brevity) is revised. The material is represented by cores from numerous boreholes in the Vorkutskoye and Seydinskoye fields in the Komi Republic, Russia.

The locality belongs to the Vorkuta Group of the Pechora Coal Basin. Insects were found in two formations of this group, Lekvorkuta Formation and the younger Inta Formation. The material on insects described in this work comes from packages (subformations) I and Ia of the Inta Formation. Almost all Blattinopsidae of the Vorkuta Group originate from these packages (middle part of the Inta Formation). From the underlying Lekvorkuta Formation, remains of two blattinopsids have been recorded (Rasnitsyn et al., 2005).

We assign one fossil from package N of the Rudnitskaya Subformation to Insecta *incertae sedis*. The second specimen from the same subformation (package unknown) is a fragment of a forewing of Blattinopsidae. This fragment is not described, but it differs from the species described in this work in the simple posterior branch of CuA (Fig. 1g; pl. 7, fig. 7). In *Glaphyrophlebia vorkutensis* sp. nov., *G. borea* sp. nov.,

and *G. komia* sp. nov. this vein branches. This specimen is most similar to *G. subcostalis* from Soyana, from which it differs in the narrow (equal in width to the interrarial) costal area behind the apex of SC. In *G. subcostalis*, this field is twice as wide as the interrarial one (Aristov and Rasnitsyn, 2021). The deposits of the Vorkuta Group are attributed to the Ufimian Stage (Lozovsky et al., 2009). However, there are different opinions on the age of this series. Either it entirely belongs to the Kungurian Stage (Pukhonto and Fefilova, 1982; Kotlyar et al., 2004; Henderson et al., 2012), or the Lekvorkuta Formation belongs to the Kungurian Stage, while the Inta Formation belongs to the Ufimian Stage (Vodolazskaya et al., 2013). The range and status of the Ufimian Stage and its boundary with the Kungurian Stage remain the subject of heated debate (Lozovsky et al., 2009). We accept the Kungurian and Ufimian stages in their traditional volume, referring to the latter the Solikamskian and Sheshmian horizons. In this work, we, with some degree of convention, attribute the Lekvorkuta Formation to the Kungurian Stage, and the Inta Formation to the Ufimian Stage. Deposits of the Pechora Group were formed in the humid, warm temperate marine climate, north of other large localities of the uppermost lower–lowermost Middle Permian. Vorkuta was located at a paleolatitude of 39.5° N, Chekarda, Tyulkino, and Soyana were at

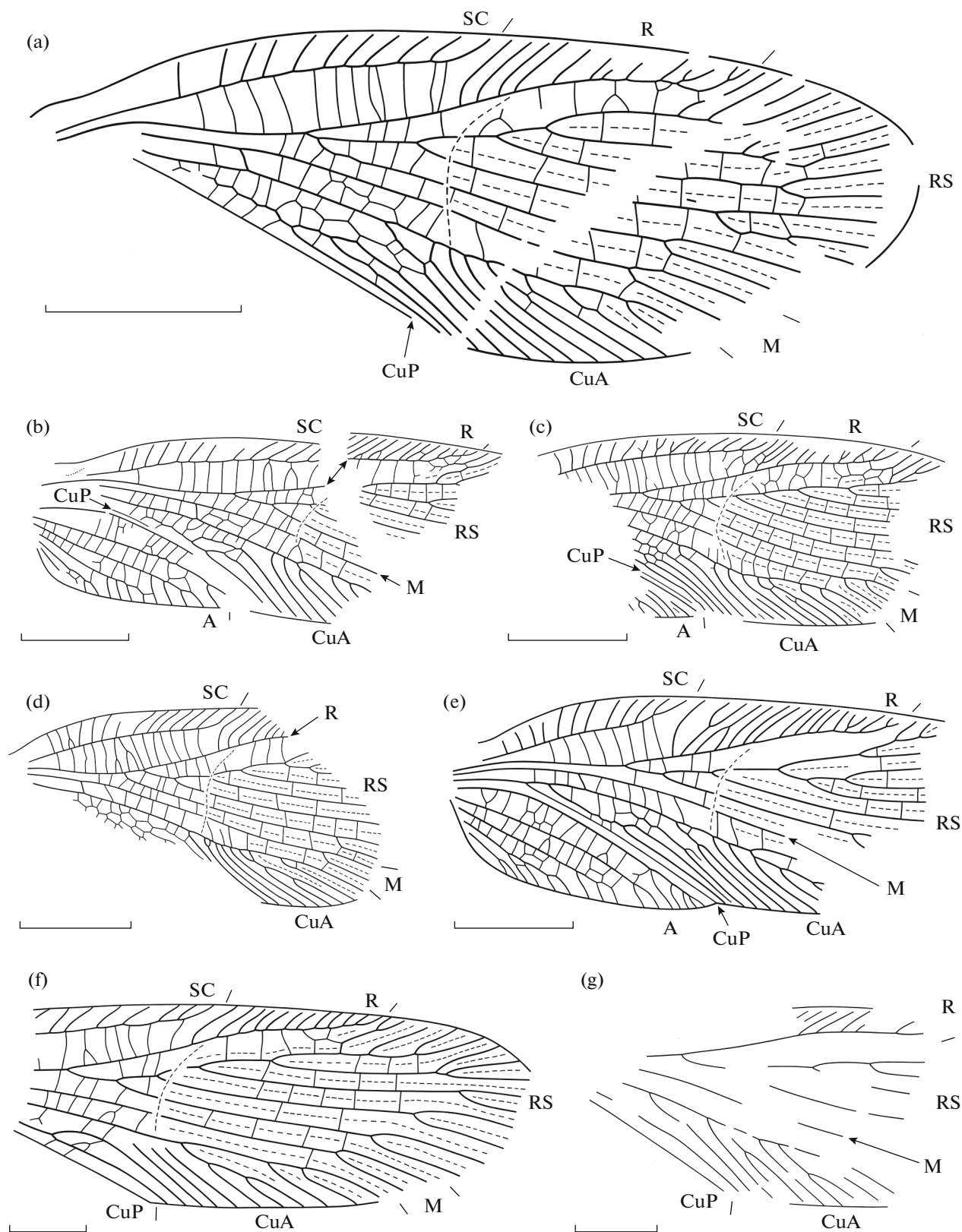


Fig. 1. Representatives of Blattinopsidae from the Vorkuta Coal Field (Middle Permian of Russia), forewings: (a–c) *Glaphyrophlebia komia* sp. nov.: (a) holotype PIN, no. 1631/157; (b) specimen PIN, no. 1631/132; (c) specimen PIN, no. 1631/497; (d) *G. vorkutensis* sp. nov., holotype PIN, no. 1631/154; (e, f) *G. borea* sp. nov.: (e) holotype PIN, no. 1631/148; (f) specimen PIN, no. 1631/128; (g) *Glaphyrophlebia* sp., specimen PIN, no. 1206/19. Scale bar (a–e) 2 mm; (f, g) 1 mm.

30.6° N, 31.9° N, and 33.2° N, respectively. The last three localities were characterized by a semiarid climate (Shcherbakov, 2008), Chekarda, Tyulkino, and Soyana had a coastal (lagoon or delta) origin (http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=122753, no = 103639 and no = 104992, respectively). The Vorkuta deposits were lagoon-marine or lagoon-lacustrine, and by the Inta time, the marine influence greatly decreased. Sediments of Horizon Ia, from which most blattinopsids are known, were formed in a fresh-water basin (Pukhonto and Fefilova, 1982).

Blattinopsidae in the Vorkuta Group make up 12% of insect remains. However, they were all found in packages I and Ia (except for one specimen from the Lekvorkuta Formation). In these packages, Blattinopsida account for 46% of insect remains. In contrast to the Blattinopsidae, with only the exception of those confined to the same stratigraphic level, the other orders of insects are more evenly stratigraphically distributed over the Vorkuta Group.

Three new species of the genus are described below: *Glaphyrophlebia* (Blattinopsidae): *G. komia* sp. nov., *G. vorkutensis* sp. nov., and *G. borea* sp. nov. Earlier, from the Vorkuta locality, blattinopsids were indicated as belonging to *G. subcostalis* (Martynov, 1928), described from the Soyana locality (Rasnitsyn, 1980a). We redescribed this species (Aristov and Rasnitsyn, 2021), and it is shown below that the material from Vorkuta belongs to separate species. Most of the definable material belongs to *G. komia*, the rest of the species are isolated. A similar situation is observed in Soyana, all identifiable blattinopsids belong to *G. subcostalis*, while *G. iva* Aristov et Rasnitsyn, 2021 is known only from the holotype (Aristov and Rasnitsyn, 2021).

COMPARATIVE ANALYSIS OF FLORA OF THE KUNGURIAN AND UFIMIAN (ROADIAN) STAGES OF PECHORA CISURALIA AND MIDDLE CISURALIA

Despite the relative geographical proximity of the Pechora Cisuralia and Middle Cisuralia, the Permian floras of these regions differ very significantly. The Permian flora of the Pechora Coal Basin and nearby sections of the Pechora Urals region has a completely distinct Angaran appearance (Zalessky and Chirkova, 1938; Pukhonto and Fefilova, 1982; Poletaeva and Pukhonto, 1990; Pukhonto, 1998; Isaev et al., 2018; see here Fig. 2 and Plate 8).

It is dominated by the remains of the gymnosperms of the order Vojnovskyales, which in recent years has been classified within a separate class Vojnovskyopsida, with characteristic “cordate-like” lanceolate leaves and very peculiar reproductive organs. The second most common group of higher plants, the remains of which may dominate in semiaquatic phytocoenoses, are

horsetails (Equisetophyta), represented mainly by species belonging to the family Tchernoviaceae.

In addition to Equisetophyta, but less commonly, the same localities contain ferns, mainly gleicheniaceans (genera *Tumidopteris* Naug. and *Prynadaeopteris* Radczenko emend. Naug.), less commonly, Marattiaceae (representatives of the genus *Corsinopteris* Doweld, which needs revision). The Inta (Lower Ufimian, Roadian) deposits of the section on the left bank of the Kozhim River downstream of the village of Kozhim-Rudnik, the oldest reliable remains of Osmundaceae ferns were found (*Todites lobulatus* Naug; for more details see: Naugolnykh, 2002).

The taxonomic diversity of the Kungurian flora in the stratotype area (Middle Cisuralia) is extremely high. We know the Kungurian flora from a number of localities, some of which are deservedly considered as specially protected natural areas (for example, the internationally acclaimed Chekarda section). Of no less importance is the whole complex of localities located near the village of Matveevo in the Perm Region, on both banks of the Barda River (Naugolnykh, 2014). The Kungurian flora of the Middle Cisuralia contains representatives of all the main groups of higher plants characteristic of the Late Paleozoic, with very few exceptions.

The main distinguishing feature of the floristic assemblages of the upper part of the Lower Permian (Kozhim-Rudnik and Lekvorkuta Formations and their equivalents) and the lower part of the Middle Permian (Inta Formation) of Northern Cisuralia, in comparison with fossil floras from synchronous deposits of the Middle Cisuralia, is the almost complete absence of conifers and peltasperms. Single finds of representatives of these groups in the Lekvorkuta, Kozhim-Rudnik, and Inta formations of the Pechora Cisuralia are very doubtful and require detailed verification. For example, in some cases shoots of Bryopsida mosses were taken for the remains of conifers. Callipterids, represented by several species of the genus *Permocallipteris* Naug., of which *P. adzvensis* (Zalessky) Naug is the most widespread, and by the genera *Comia* Zalessky and *Compsopteris* Zalessky, appear in the Pechora Coal Basin and in the Pechora Cisuralia much later, in the Kazanian (i.e., in the Wordian). This was due to the migration of these plants in the second half of the Permian period from the Middle and Southern Cisuralia toward north and northeast, to the outer limits of Angarida s.s. These differences were most likely due to different paleoclimatic conditions in which the Permian floras of the Middle Cisuralia and the Pechora Coal Basin developed, including the regions of the Pechora Cisuralia. The climate of the Middle Cisuralia in the late Early and early Middle Permian was distinctly semiarid, seasonally dry, which is emphasized by the presence of xerophilic elements [relict calamite *Calamites gigas* Brongn. (for more details on the paleogeographic his-

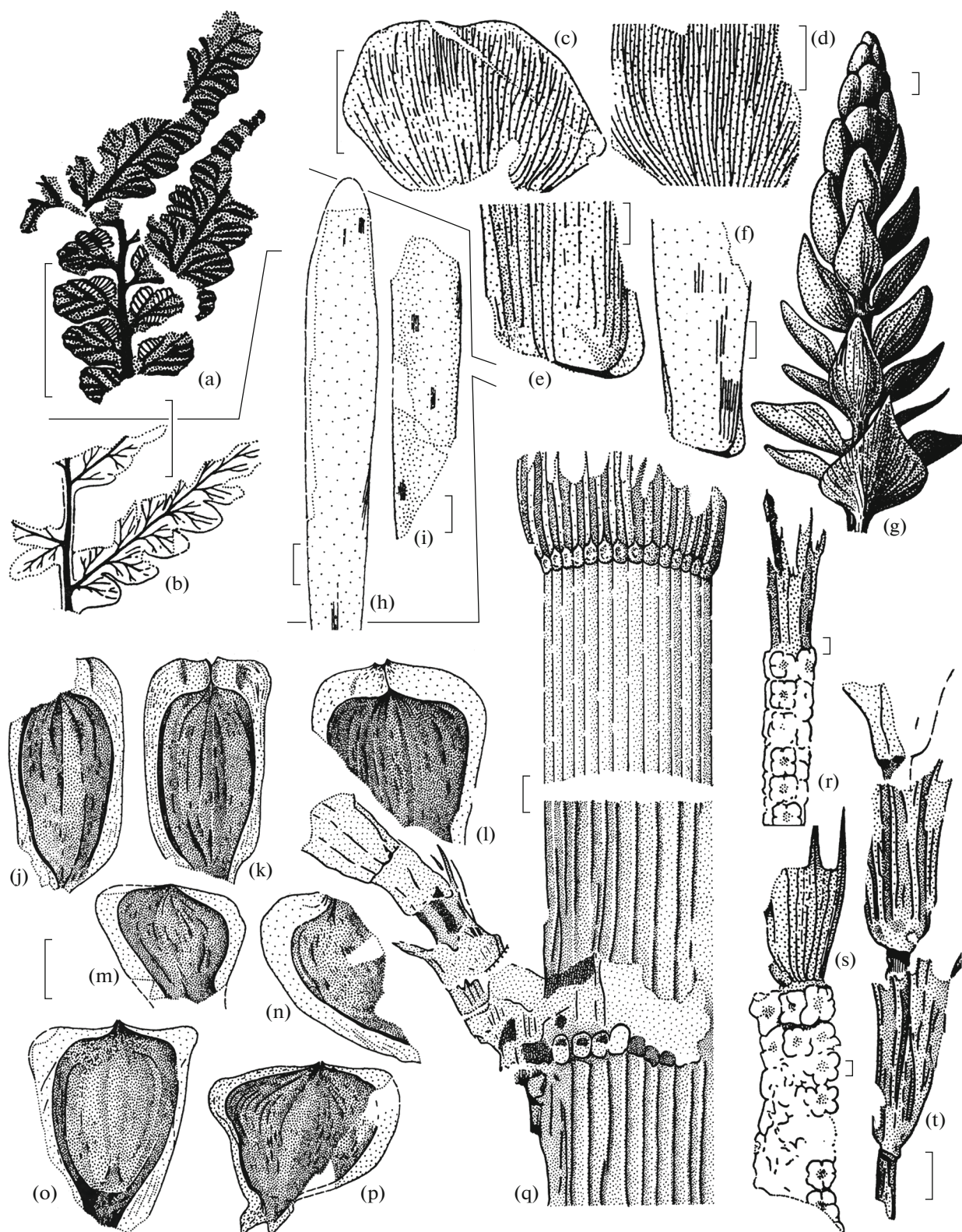
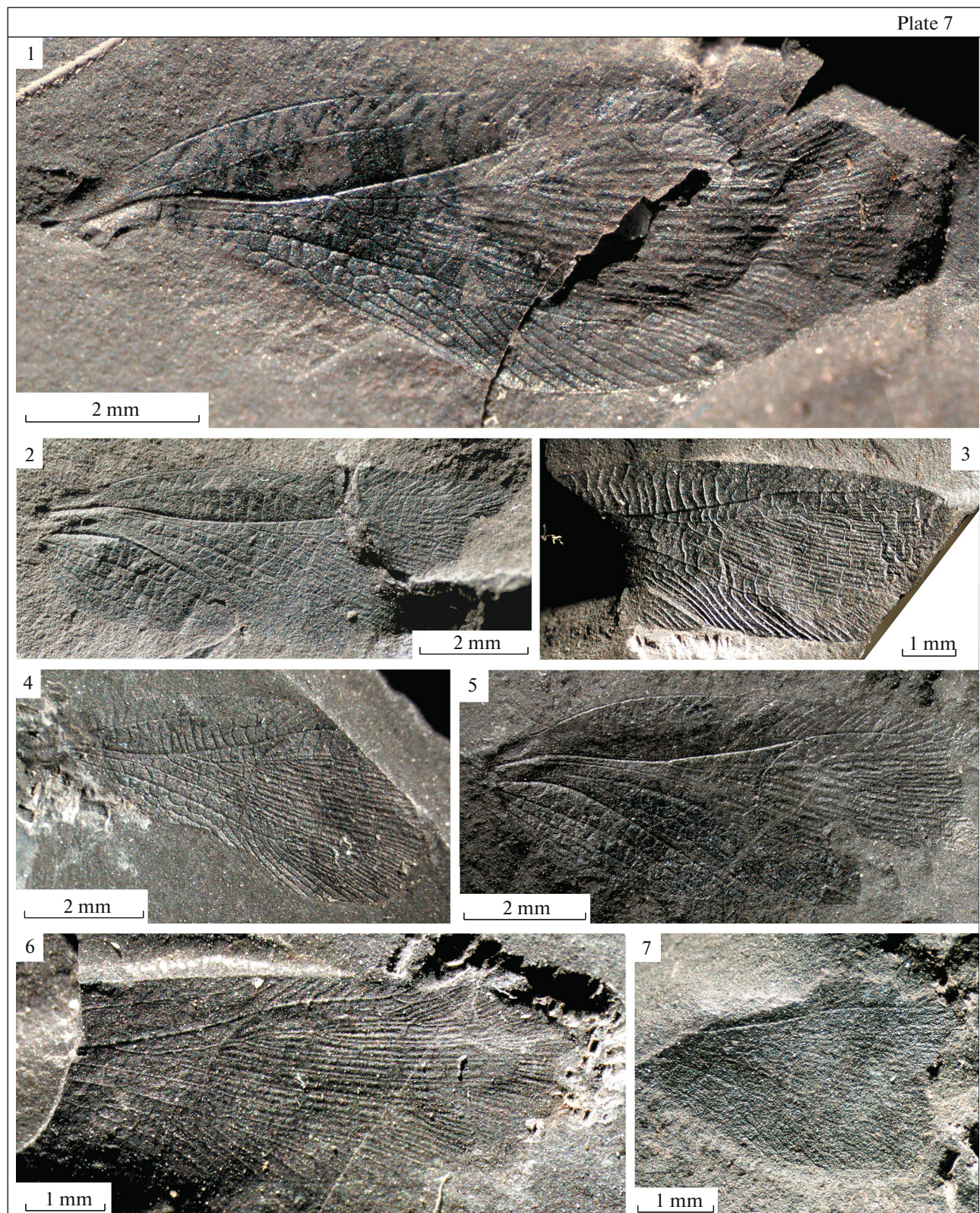


Fig. 2. The most characteristic representatives of the Kungurian (Kozhim-Rudnik Formation, locality Kozhim-4) and Ufimian (Inta Formation, Kozhim-5) floras of the Kozhim Section (Pechora Cisuralia): (a) *Corsinopteris semiliberus* (Naug.) Doweld, Marattiaceae; (b) *Pecopteris* cf. *borealis* Zalesky, fern frond fragment; (c, d) *Nephropsis* (*Sulcinephropsis*) sp., scale-like leaf of Voinovskiales; (e, f) *Rulfloria* (*Alatorulfloria*) aff. *derzavini* (Neuburg) S. Meyen; (g) reconstruction of the apical part of the Voinovskiales shoot, based on materials from the Kozhim-5 locality; (h, i) *Rulfloria* (*Alatorulfloria*) cf. *recta* (Neuburg) S. Meyen; (j–p) seeds of *Samaropsis vorcutana* Tschirkova; (q–t) equisetophyte *Paracalamitina striata* Zalesky emend. Naug. Locality: Kozhim-5 (a–g; j–p; q–t); Kozhim-4 (b, h, i); locality details see in Naugolnykh (2007). Scale bar 1 cm (a–i); 2 mm (j–t).



Explanation of Plate 7

Figs. 1–3. *Glaphyrophlebia komia* sp. nov., forewings: (1) holotype PIN, no. 1631/157; (2) paratype PIN, no. 1631/132; (3) specimen PIN, no. 1631/497.

Fig. 4. *Glaphyrophlebia vorkutensis* sp. nov., holotype PIN, no. 1631/154, forewing.

Figs. 5, 6. *Glaphyrophlebia borea* sp. nov., forewings: (5) holotype PIN, no. 1631/148; (6) specimen PIN, no. 1631/128.

Fig. 7. *Glaphyrophlebia* sp., specimen PIN, no. 1206/19, forewing; Russia, Komi Republic, Vorkuta Coal Field; Middle Permian, Ufimian Stage).

tory of this species, see: Naugolnykh, 2005)], callipterids, walchian conifers (*Walchia appressa* Zalessky, *W. bardaeana* Zalessky emend. Naug.), the first representatives of Voltzian conifers (genus *Archaeovoltzia* Naug.). The seasonally dry climate of the Middle Cisuralia at the end of the Early Permian is suggested by the huge series of Kungurian evaporites (sulfates of the Irenian Regional Substage, as well as deposits of rock and potassium salts of the Bereznikovskiy Mines). The presence of a hot and dry climate on the territory of the Middle Cisuralia in the Ufimian is supported by the numerous glyptomorphs of rock salt and intergrowths of gypsum crystals (“gypsum suns”), which are widespread in the sediments of the Solikamsk Regional Substage in the basin of the Chusovaya and Sylva rivers. Apparently, it was the warm climate that contributed to the growth of arboreal Lycopodiophyta of a distinctly thermophilic appearance, attributed to the genus *Ufadendron* Naug., in Middle Cisuralia. Representatives of this genus were also found in the zone of development of Permian low latitude vegetation (Tang et al., 2020).

In contrast to Middle Cisuralia, the climate in the middle of the Permian Period in the Pechora Cisuralia was significantly more humid and, possibly, cooler. This was reflected in active peat and coal formation in the Pechora basin, as well as in the absence of known xerophytes (callipterids, walchian conifers) in the sediments of the Lekvorkuta, Kozhim-Rudnik, and Inta formations.

Those plants that are present in the floras of both regions (Sphenophyllales, see Naugolnykh, 2015b), the horsetail family Tchernoviaceae, in particular, the genus *Annulina* Neuburg (for more details see: Naugolnykh and Mogilnikova, 2018), either grew in intrazonal near-water vegetation, or had wide ecological amplitudes (for example, Vojnovskyopsida). The same trends continued in the Kazanian, in particular, in the Soyana flora (Naugolnykh, 2015a). In the most general terms, the Early Permian vegetation that existed in the areas corresponding to the present-day position of the Subpolar and Northern Urals and Cisuralia appears somewhat more archaic than that of Middle Cisuralia, where there are many evolutionarily advanced taxa, such as various ginkgophytes and Angiopeltaceae. The Inta Formation of the Vorkuta section, as well as the corresponding deposits in the Kozhim section, includes a large number of Vojnovs-

kyopsida leaves (the remains of this group dominate among plants); however, they were not an important trophic resource for insects. Before the Cretaceous (before angiosperms), gnawing phyllophages were almost absent among insects: there were consumers of seeds, fruits, and wood, as well as sucking phytophages on vegetative parts of plants (Rasnitsyn and Quicke, 2002).

SYSTEMATIC PALEONTOLOGY

Order Blattinopsida

Family Blattinopsidae Bolton, 1925

Genus *Glaphyrophlebia* Handlirsch, 1906

Glaphyrophlebia komia Aristov, Rasnitsyn et Naugolnykh, sp. nov.

Plate 7, figs. 1–3

E t y m o l o g y. From the Komi Republic.

H o l o t y p e. PIN, no. 1631/157, part and counterpart imprints of an incomplete forewing; Komi Republic, Pechora Coal Basin, basin of the Vorkuta River, Vorkuta Field, well core K-1143, depth. 258.8 m; Middle Permian, Ufimian Stage, Vorkuta Series, Inta Formation, Package I, horizon Ia

D e s c r i p t i o n (Figs. 1a–1c). Small insects. The costal area at the base of RS is half the width of the subcostal area. SC ends just after mid-wing. Stem R is S-shaped curved at its apex. RS begins at the border of the basal third of the wing, departs from R with one stem, with five to seven main branches and with 14 or more endings. The main branches of RS are not forked. M₅ enters CuA after its fork; M is simple, with two or three endings. CuA has 10–14 branches, the “posterior” branch of CuA forms a comb of three to four branches. CuP is straight, A₁ is simple, A₂ has five branches and more than 13 endings. The transverse veins are simple, Y-shaped, and can form a double row of cells in the medial and intercubital fields.

M e a s u r e m e n t s in mm: forewing length 9.5–11.

C o m p a r i s o n. *G. komia* sp. nov. is most similar to *G. borea* sp. nov. from the Vorkuta Coal Field, from which it differs in the narrow costal area and abundantly branching “posterior branch” of CuA. In *G. borea*, the costal area at the base of RS is slightly narrower than the subcostal area, the “posterior” branch of CuA has two terminations. The new species differs from *G. subcostalis* in a narrow costal area and a

Explanation of Plate 8

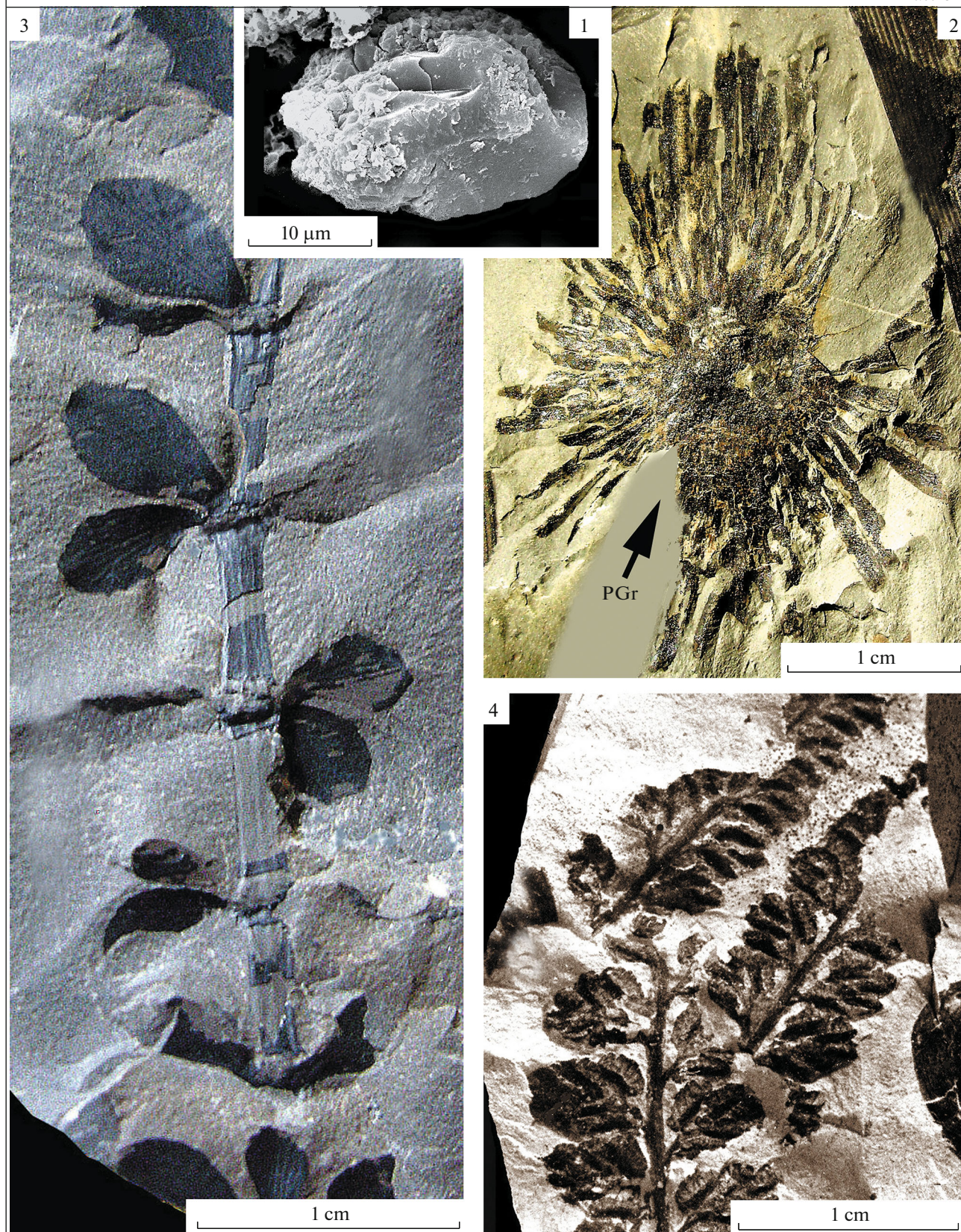
Fig. 1. One of the pollen grains extracted from microsporangia of a *Vojnovskya*-like reproductive organ, figured here in Pl. 8, fig. 2.

Fig. 2. *Vojnovskya*-like reproductive organ, PGr—the area from which the pollen grains were extracted; Russia, Komi Republic, Kozhim-4 locality; Lower Permian, Kungurian Stage.

Fig. 3. *Sphenophyllum comiense* Tschirkova, leafed shoot of *Sphenophyllum*; Russia, Komi Republic, Kholmeryu Field, Borehole Kh-157, depth 400 m; middle Permian, Ufimian Stage.

Fig. 4. *Corsinopteris semiliberus* (Naug.) Doweld, Marattiaceae; Russia, Komi Republic, Kozhim-5 locality; Middle Permian, Ufimian Stage.

Plate 8



comb-like “posterior” branch of CuA. In *G. subcostalis*, the costal area is 0.67 of the width of the subcostal area, the posterior branch of CuA has two endings (Aristov and Rasnitsyn, 2021).

Material. In addition to the holotype, three specimens from Horizon I of the Vorkuta deposit: specimen PIN, nos. 1206/21, 25, 31; 21 specimens from Horizon Ia of the same deposit: specimen no. PIN, nos. 1206/22; 1631/127, 129, 130, 131, 132, 137, 138, 141, 143, 149, 151, 157, 158, 262; 263; 264, 356, 495, 496, 497, 499 and one specimen (PIN, no. 1631/502) from Horizon I of the Seydinskoe Coal Field.

Glaphyrophlebia vorkutensis Aristov, Rasnitsyn et Naugolnykh, sp. nov.

Plate 7, fig. 4

Etymology. From the Vorkuta Coal Field.

Holotype. PIN, no. 1631/154, part and counterpart imprints of an incomplete forewing; Komi Republic, Vorkuta Coal Field, core of Borehole K-1143, depth 258.8 m; Middle Permian, Ufimian Stage, Inta Formation, Horizon Ia.

Description (Fig. 1d). Small insects. The anterior margin of the forewing is convex in its basal half. The costal area at the base of RS is narrower than the subcostal. SC ends before the level of the apex of CuP, curved parallel to the anterior edge of the wing. RS begins before the border of the basal third of the wing, extends from R by two stems. The anterior one has more than seven branches, the posterior one has a short terminal fork. The main branches of RS, except for the front, are forked. M is simple, with a short terminal fork. CuA begins to branch after the confluence with the M_5 , irregularly combed, with 10 branches. The transverse veins are simple and Y-shaped, forming rows of cells at the base of the intercubital field.

Measurements in mm: length of the preserved fragment is 6.7; estimated length of the forewing is 9.5.

Comparison. *G. vorkutensis* sp. nov. is the most similar to *G. uralensis* (Martynov, 1940) from the Lower Permian Chekarda locality (Kungurian Stage of the Perm Region, Russia), from which it differs in the short SC. In *G. uralensis*, the SC ends behind the level of the CuP summit (Rasnitsyn, 1980). The new species differs from *G. subcostalis* (Martynov, 1928) in RS, which extends from R in two stems. In *G. subcostalis*, RS extends with one stem (Aristov and Rasnitsyn, 2021).

Material. Holotype.

Glaphyrophlebia borea Aristov, Rasnitsyn et Naugolnykh, sp. nov.

Plate 7, figs. 5, 6

Etymology. From the Greek βόρειο (northern).

Holotype. PIN, no. 1631/148, part and counterpart imprints of an incomplete forewing; Komi Republic, Vorkuta Coal Field, core of Borehole

K-1006, depth 420.8–425.2 m; Middle Permian, Ufimian Stage, Inta Formation, Horizon Ia.

Description. (Figs. 1e, 1f). Small insects with wide forewings (the length of the forewing is about 2.8 times its width). The anterior margin of the forewing is convex. Costal area at the base of RS is slightly narrower than subcostal area; SC is slightly S-shaped curved, terminating before the mid-wing or at its middle. R is with a slight S-bend. RS begins at the border of the basal third of the wing, extends from R in one stem, not always regularly comb-like directed backward, with more than 10 branches. The main branches of RS are forked. M_5 enters CuA after its division into branches; M has a terminal fork only. CuA has more than 11 branches, the base of one of them is lost among crossveins, the posterior one (extending from CuA prior to its confluence with M_5) has a distinct simple fork. CuP is straight. The clavus is small, A_1 is simple, with five branches at the top, A_2 with four branches and 11 ends. The crossveins are simple, Y- and H-shaped in the clavus and forming a double row of cells between the branches of CuA and the anal veins.

Measurements in mm: length of the preserved fragments of the forewing of the holotype is 8.3; estimated length of the forewing is 9–10.

Comparison. The new species is most similar to *G. subcostalis* (Martynov, 1928) from the Middle Permian locality of Soyana (Kazanian Stage; Arkhangelsk Region, Russia), from which it differs in a distinct fork on the posterior branch of CuA. In *G. subcostalis*, the fork is disintegrated and branches extend from the crossveins (Aristov and Rasnitsyn, 2021).

Material. Apart from the holotype, specimens PIN, nos. 1613/126, 128 from the type locality.

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