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A new peltaspermaceous pteridosperm from the Upper Permian of the Russian Platform

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ABSTRACT

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The paper focuses on the description of a new species of peltaspermalean pteridosperm *Peltaspermopsis polyspermis* Naug. sp. nov. The plant remains were collected from the Upper Permian (Tatarian) of northern part of Russia (N. Dvina River Basin). The species is characterized both by reproductive organs (seed bearing discs and their racemose aggregations) and vegetative organs (stems with nodes of seasonal growth interruptions and *Pursongia*-like lanceolate leaves). The new combination *Peltaspermum parvulum* (Sixtel) Naug. comb. nov. is proposed. General questions concerning *Pursongia* Zalessky, its taxonomical composition, morphological features and relationship with *Glossopteris* are discussed. The species *Pursongia amalitzkii* Zalessky is described on the base of newly collected material.

Key-words—Permian, Pteridosperms, Seed bearing discs, Leaf morphology, *Pursongia, Glossopteris.*

रूसी क्षैतिज आधारभूमि (प्लेटफ़ार्म) पर उपरि परमियन कल्प के नवीनतम पेल्टास्पर्मेशियस टेरिडोस्पर्म

सर्गेइ वी. नाउगोलिन्ख

सारांश

प्रस्तुत शोध-पत्र में पेल्टास्पर्मेलियन टेरिडोस्पर्म की एक नई प्रजाति पेल्टास्पर्माप्सिस पॉलीस्पर्मिस नाउग नव प्रजाति का विवेचन अभिप्रेत है। इस हेतु पादप अवशेष रूस के उत्तरी भाग (एन.ड्वाइन नदी द्रोणी) के उपरि परमियन (तातारियन) कल्प से संग्रहीत किए गए। प्रजाति जननांगों (बीजधारी बिम्ब तथा उनके सभी असीमाक्षी) तथा वनस्पतिपरक अंगों (मौसम वृद्धि अवरोधकों से युक्त गाँठों वाले तने तथा *परसोंगिया* की भाँति की मालाकार पत्तियाँ) दोनों द्वारा ही निरूपित है। अतः नवीनतम संयोजन *पेल्टास्पर्मम* पार्व्यूलम (सिक्सटेल) नाउग. नव संयोजन प्रस्तावित किया जाता है। इसके अतिरिक्त *परसोंगिया* ज़ैलैक्सी की कुछ सामान्य सी शंकाओं, जैसे- इसका वर्गिकीय संघटन, संरचनात्मक अभिलक्षण तथा *ग्लॉसोप्टेरिस* के साथ इसके सम्बन्धों के समाधान ढूँढने के भी प्रयास इस शोध पत्र में किए गए हैं। नवीनतम संग्रहीत पदार्थों के आधार पर *परसोंगिया अमालिट्ज़काई* नामक प्रजाति का भी विवेचन किया गया है ।

संकेत शब्द—परमियन, टेरिडोस्पर्म, बीजधारी बिम्ब, पर्णसंरचनाविज्ञान, परसोंगिया, *ग्लॉसोप्टेरिस.*

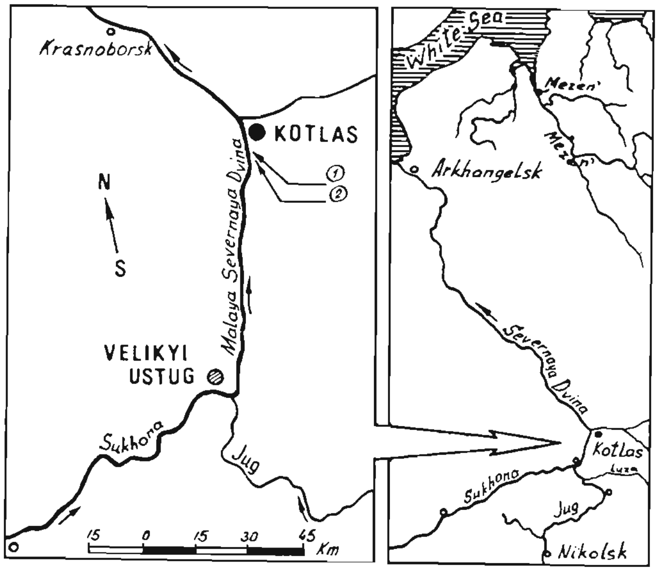

Fig. 1—Geographical position of the localities studied 1- Sokolki. 2- Zavrajie.

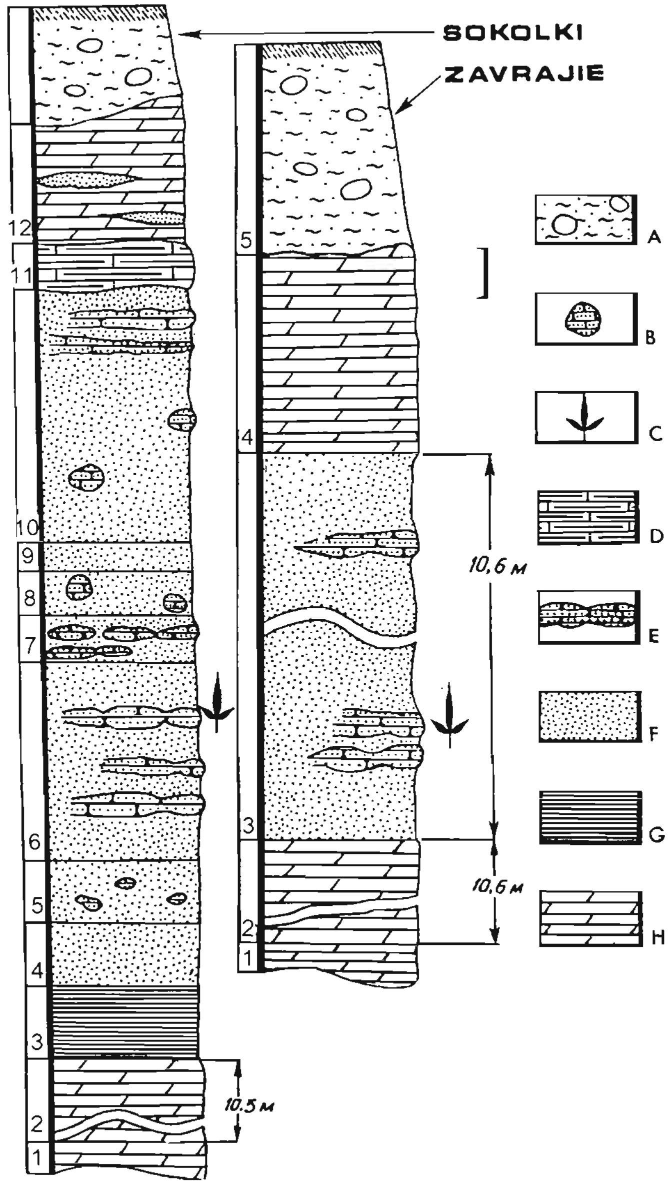

Fig. 2—Stratigraphical sequences of the localities studied. I -Sokolki. II - Zavrajie. Legend: A - quaternary glacial sands and clays, B - spheroid sandstone concretions, C - plant remains, D - marl or argillite with the big amount of carbonate material, E - flattened sandstone concretions, F - sand lenses, G - argillite, H - marl. Scale - 1 m.

INTRODUCTION

INVESTIGATION of the Upper Palaeozoic plants of Angaraland is an interesting and important problem for modern palaeobotany, since Angaraland (including Subangaraland ecotonic belt) floras are quite distinctive and considerably different from taxonomic assemblages from other phytogeographical provinces of that time.

The representatives of Peltaspermales were widely spread along exterior parts of the Angaran continent. There, they were the most abundant plants and represented by high diversity of taxa.

The aim of this paper is the description of a peltaspermalean pteridosperm, which is assigned to new species *Peltaspermopsis polyspermis* Naug., sp. nov. In addition some questions of taxonomy and nomenclature of *Pursongia*-like leaves are discussed.

MATERIAL AND METHODS

The specimens studied originated from two famous localities of plant remains, which belong to the stratotype section of Severodvinskian Horizon of Upper Tatarian substage

PLATE 1

Peltaspermopsis polyspermis Naug. sp. nov.
Seed-bearing discs (1-3, 7-9) and sterile leaves (4-6).

1-2. Cross section through the disc stalk with different focus. Specimen no. 4851/3a;

3, 8. Racemose polysperm, upper disc shows well preserved seed scars. Specimen no. 4851/3;

7. Seed-bearing disc with numerous (24) radial sectors. Specimen no. 4851/2;

9. Margin of the disc with the preserved seed scars. Specimen no. 4851/2.

4-6. Simple lanceolate leaves of Pursongia-type, associated with the seed-bearing discs. Specimen no. 4851/10 (4, 5) and 4851/12 (6). Zavrajie locality. Magnification: x 5 (1-3, 7-9), x 3 (4-6).

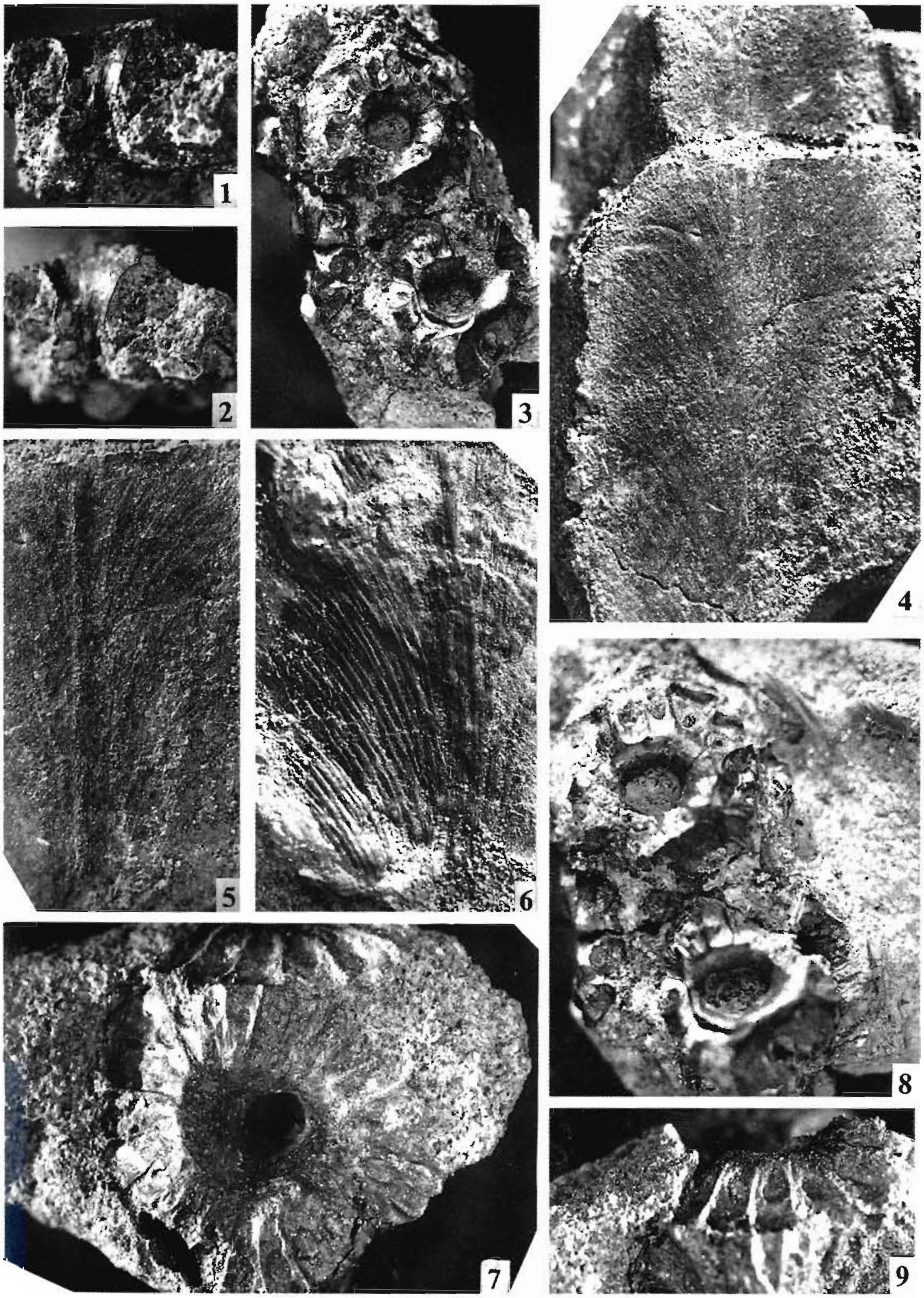

PLATE 1

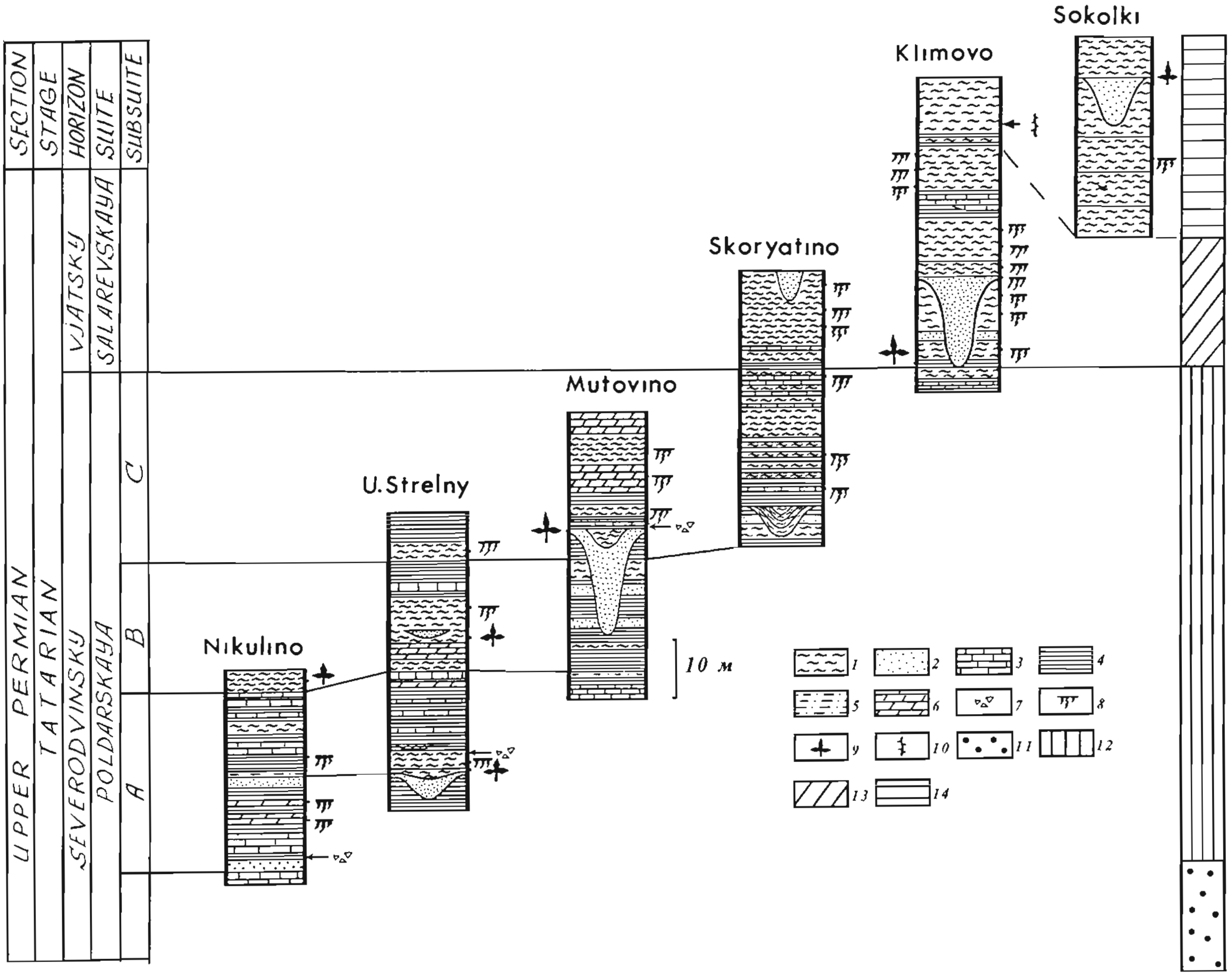

Fig. 3—Correlation between localities studied and the other Tatarian outcrops of the Sukhona-Northern Dvina Basin. Legend: 1 - Clayly aleurolites, 2 - Sands and sandstones, 3 - Mudstone, 4 - Sandy clays, 5 - Sandstones with small influx of aleurolites and argillites, 6 - Marls, 7 - Breccia, 8-9 - Root remains of several types, 10 – Plant megafossils (leaves, stems, fructifications), 11 - Basin deposits of Sukhonskaya Suite, 12 - Subaquious and subaerial deposits of shallow waters and coast lowlands of Poldarskaya Suite, 13 - Paleosol horizons in the lower part of Salarevskaya Suite, 14 - Desert lake sediments with postdiagenetic carbonate encrustations, upper part of Salarevskaya Suite (after Arefiev & Naugolnykh, 1998).

(Gomankov & Meyen, 1986; Arefiev & Naugolnykh, 1998). The localities are disposed on the right bank of the Small Northern Dvina, 10 km upstream of Kotlas City (Fig. 1). Both localities have historical names "Sokolki" and "Zavrajie" (Amalitzky, 1897, 1901, 1922-1924).

These localities are sand and sandstone lenses, which are disposed in marl and clay sediments (Figs 2, 3). The plant remains were found in middle parts of the lenses and, as a rule, occurred in concretions or slightly less consolidated sandstones (Fig. 2).

The specimens were studied under Binocular Microscope MBS-9 and Scanning Electron Microscope Stereoscan 600. Figures were made from photographs (Figs. 7, 11 A-F) and under a binocular microscope with the use of an ocular with grid (Figs 4A-C, E, G-H, J, 5, 7).

The collection is stored in the Geological Institute of the Russian Academy of Sciences (GIN RAS, collection 4851).

SYSTEMATIC DESCRIPTION

Genus—PELTASPERMOPSIS Gomankov, 1986, emend. Poort et Kerp, 1990

1986 Gomankov & Meyen, 1986, p. 56-57.

1990 Poort & Kerp, 1990, p. 20.

Type Species—Peltaspermum buevichiae Gom. & Meyen, 1979; Upper Tatarian, Upper Permian of the Russian platform.

Generic Diagnosis—(after Poort & Kerp, 1990, slightly modified): Genus is used as natural. It includes both vegetative and reproductive organ characteristics. Seed bearing or-

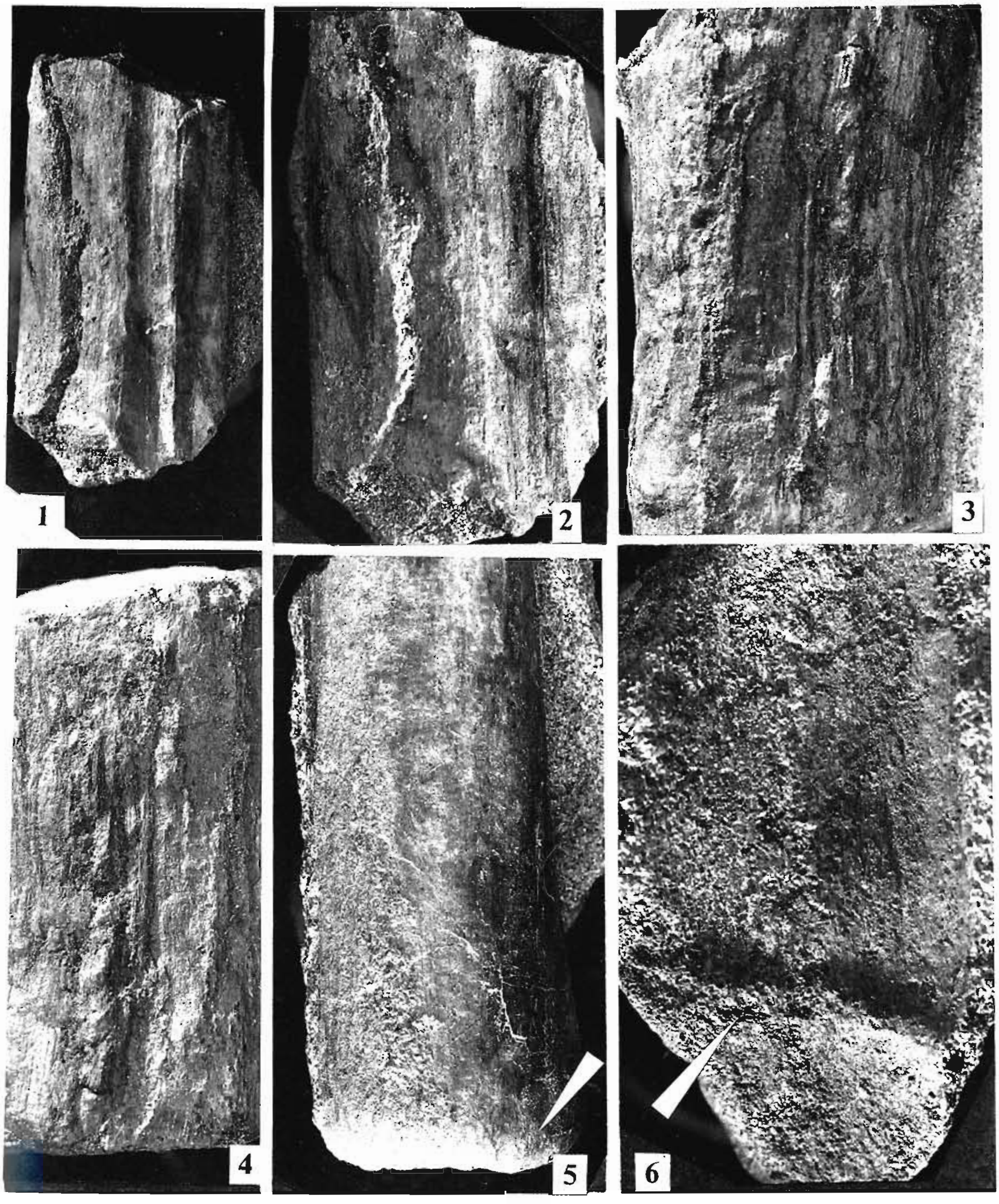

PLATE 2

Peltaspermopsis polyspermis Naug. sp nov.

Stem fragments. The seasonal growth interruptions are pointed out by the arrows. Specimen Nos. 4851/1 (1, 5), 4851/7 (3, 4), 4851/4 (2), 4851/8 (6) Zavrajie locality. Magnifications x 2 (4), x 3 (1, 2, 6), 3 x 4 (5).

gans are compound polysperms with closely disposed elliptical or radially symmetrical umbrella-shaped seed bearing discs (peltoids). Radially orientated ribs and furrows present on the disc surface. Distal ends of the ribs form marginal lobes. Seeds are attached to lower surface of the discs around central stalk.

Male fructifications consist of several prolonged elliptical sporangia, which were basally fused and form synangia. They produced *Vittatina* pollen and pollen of some closely

1	2	3	4	5	6
Triassic	*Peltaspermum parvulum* (Sixtel) Naug., comb. nov. *Peltaspermum petchoricum* Chramova	4-10 6-7	10-24 14-15	R ?	*Lepidopteris* *Scytophyllum, Lepidopteris*
Upper Permian Zechstein and Tatarian	*Peltaspermum martinsii* (Germar) Poort & Kerp *Peltaspermopsis buevichiae* Gomankov emend. Poort & Kerp *Peltaspermopsis polyspermis* Naugolnykh, sp. nov.	8-20 8-12 5-10	11-14 8-14 24	H, R H R	*Lepidopteris* (al. *Callipteris*) *martinsii* *Tatarina conspicua* *Pursongia*
Upper Permian Ka-zanian and Ufimian	*Peltaspermum nanshanense* Durante *Peltaspermum* (?) sp. A (Meyen, 1982) *Peltaspermum* Sp. (sp. nov.?) Unpublished data, from the Kazanian (?) of Russian Far-East *Peltaspermum* (?) sp. „C“, ex Pukhonto & Fefilova, 1983	6-14 10-14 10-15 5-6	16-18 15-18 15-20 8	H, R R R R	*Rhachiphyllum* (al *Callipteris*), *Compsopteris* versus *Pursongia* *Rhachiphyllum* (al. *Callipteris*) *adzvense* *Compsopteris* *Rhachiphyllum* (al. *Callipteris*) ex gr. *adzvense* ?
Lower Permian	*Peltaspermum retensorium* (Zalessky) Naug. & Kerp	6-25	8-25	H	*Rhachiphyllum* (al. *Callipteris*) *retensorium*

Fig. 4—Selected representatives of *Peltaspermum* and *Peltaspermopsis*: main characters: 1. Age, 2. Female fructifications, 3. Disc diameter (mm), 4. Number of radial sectors, 5. Type of polysperm (R-racemose, H – head-like), 6. Associated leaves.

related striated types (*Protohaploxypinus* etc).

Leaves are simple, disposed on shortened brachyblast-like and unmodified stems in spiral order. Leaf outlines are linear or lanceolate with rounded apex and narrow base. Venation is fan-shaped, with central vein cluster (false midvein). Veins are simple or twice dichotomizing. Venation, as a rule, is not clearly seen.

Distribution—Upper Permian of the Russian platform and Cis-Urals.

Species Composition—*P. buevichiae* (Gom. & Meyen) Gom. emend. Poort & Kerp, *P. polyspermis* Naug., sp. nov.

REMARKS ON GENUS COMPOSITION AND ITS COMPARISON WITH RELATED GENERA

When the genus *Peltaspermopsis* was initially established (Gomankov & Meyen, 1986) the following characteristic patterns were pointed out: (1) compact head-like disposition of peltoids around central axis; (2) relatively small seed scars; (3) relatively large distance between seed scars (distance is over the diameter of the scar). However, as it was justly noted by Poort & Kerp (1990), the type of peltoid position on the fertile axis for the type-species of *Peltaspermum* Harris (*P. rotula*) is still unknown. *P. rotula* polysperms can be

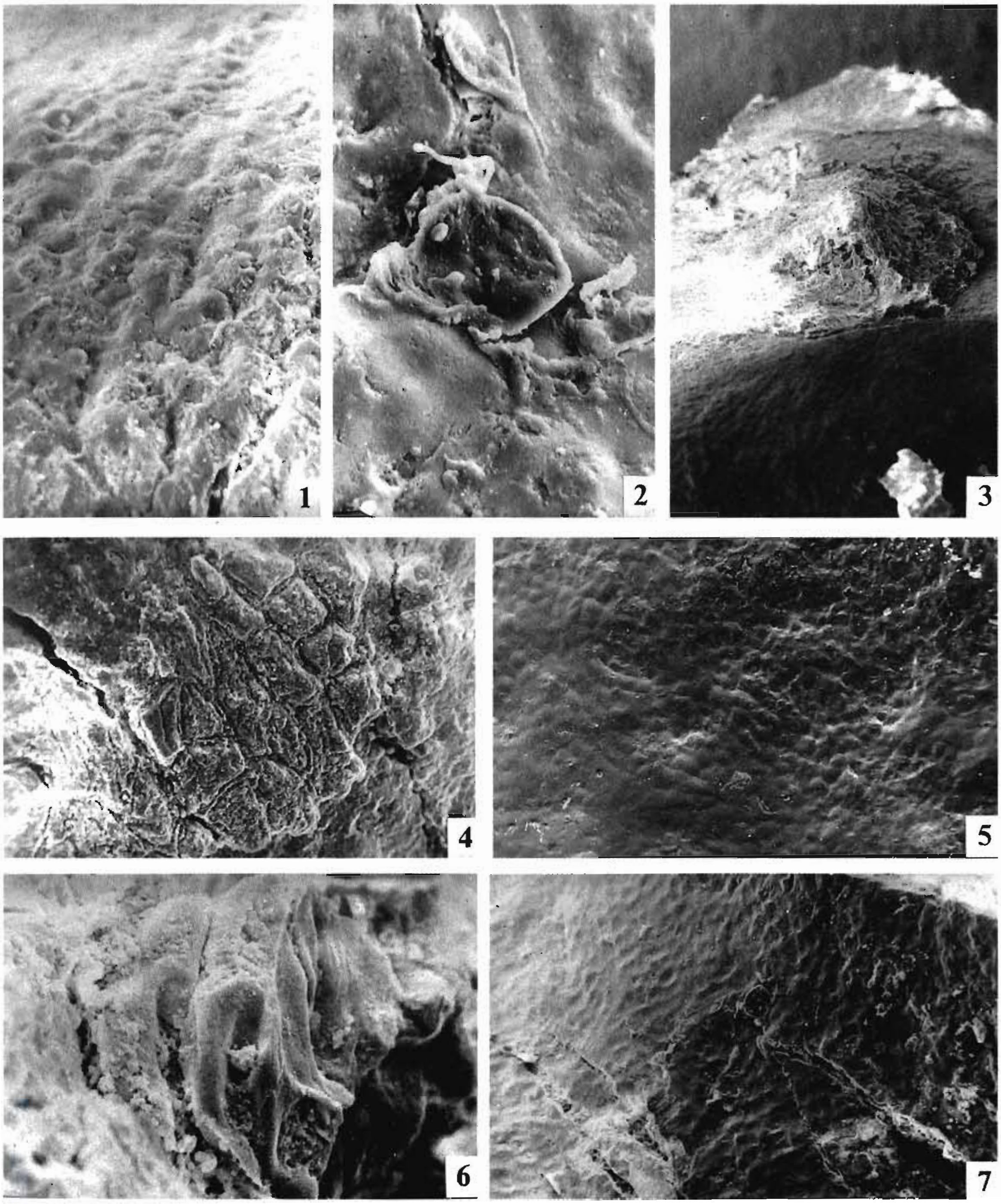

PLATE 3

Peltaspermopsis polyspermis Naug. sp. nov.
Microstructure of seed-bearing disc adaxial surface.

1, 5, 7 Polygonal almost isometrical cells of epidermis;
2, 3 Seed scar microstructure;
4, 6. Microstructure of seed-bearing disc base. Specimen No. 4851/3a. Zavrajie locality. Magnification: x 25 (2); x 50 (3), x 100 (5, 7), x 250 (1, 4), x 500 (2), x 1000 (6).

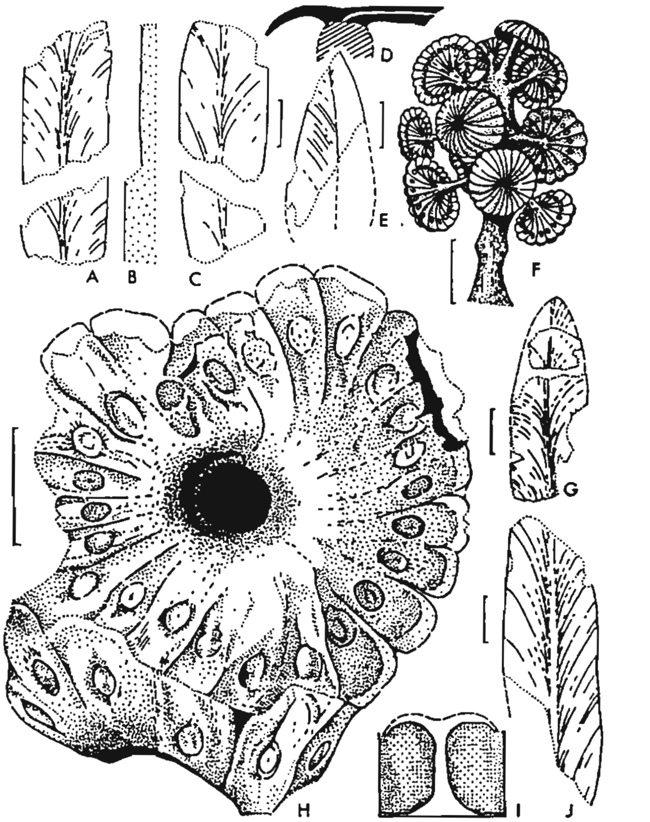

Fig. 5—*Peltaspermopsis polyspermis* Naug. Leaves and ovuliferous disc macromorphology. A-C, E, G, J - Isolated leaves, H – Seedbearing discs, D - Sketch of seed attachment, F - Polysperm reconstruction, I - Mode of preservation, matrix is dotted. Zavrajie locality. Scale bar - 1 mm (H), 1 cm (A-C, E-G, J). D, I - Without scale. Specimens: A - 4851/11a; B, C - 4851/11; E - 4851/18; F – Based on specimen 4851/3; G - 4851/10; H - 4851/2; J - 4851/14.

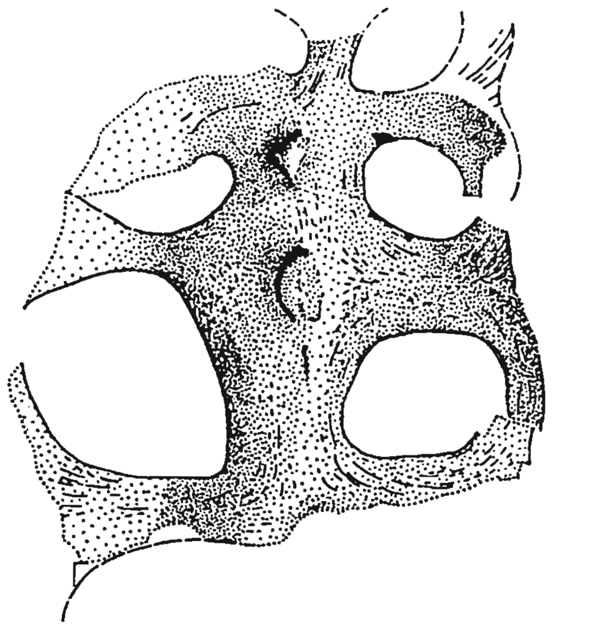

Fig. 6—*Peltaspermopsis polyspermis* Naug. Polysperm axis with attached disc stalks. Zavrajie locality. Scale bar - 1 cm. Specimen 4851/9.

both compact head-like aggregates and more lax, loose racemose ones. Both types of compound polysperms may sometimes be observed for one and the same species of peltasperm (for example, *P. martinsii*). As for other characteristics, which were used by Gomankov, it should be noted that they are very variable and in various combinations may be observed in many peltasperm species (Fig. 4). For instance, the syndrome of seed-bearing disc characteristics, which were used by Gomankov as generic for *Peltaspermopsis,* is present in *Peltaspermum incisum* Prynada (Stanislavsky, 1976). Seed-bearing discs of *P. incisum* have very small, almost crack-like seed scars with long distances between them (Stanislavsky, 1976, Pl. XXII, 5; Fig. 18). Nonetheless, this plant must be assigned to genus *Peltaspermum* (Poort & Kerp, 1990).

It is clear that *Peltaspermopsis* Gom., as it was introduced by the author of the genus, cannot be sustained on the basis of the characters that are cited in Gomankov and Meyen (1986). However, since the relationship between peltoids *Peltaspermopsis buevichiae* and simple lanceolate leaves of *Tatarina*- or *Pursongia*-type is almost well proved, this specific combination of ovuliferous structure and sterile leaves allow us to emend the diagnosis of the genus and fit it in the natural system of vascular plants generally based on reconstructed, well-documented taxa. This procedure with *Peltaspermopsis* was done by Poort and Kerp (1990), who proposed a new fuller diagnosis of *Peltaspermopsis.*

Durante (1992) did not agree with the validity of *Peltaspermopsis* sensu Gomankov either, and used it as subgenus of *Peltaspermum* Harris. As a possibility of moving *Peltaspermopsis* and *Peltaspermum* to the natural system of peltasperm genera, she set out a synthesis of all data about fructifications and associated leaves.

Schweitzer and Kirchner (1998) described a new species *Peltaspermum decipiens* and followed in general the traditional using of nomenclature and taxonomy of *Peltaspermum*-type fructifications and sterile leaves of *Lepidopteris* and *Scytophyllum* type. They criticized Poort & Kerp proposal to unite the genera, and argumented that the genera should be used independently because of uncertain correlation between *Scytophyllum*, *Lepidopteris* and *Peltaspermum*. According to my opinion, we can use both approaches: reconstructed genera *sensu* Poort & Kerp (1990) for general applications like paleophytogeography, paleoecology, and traditional formal genera for field geology and stratigraphy.

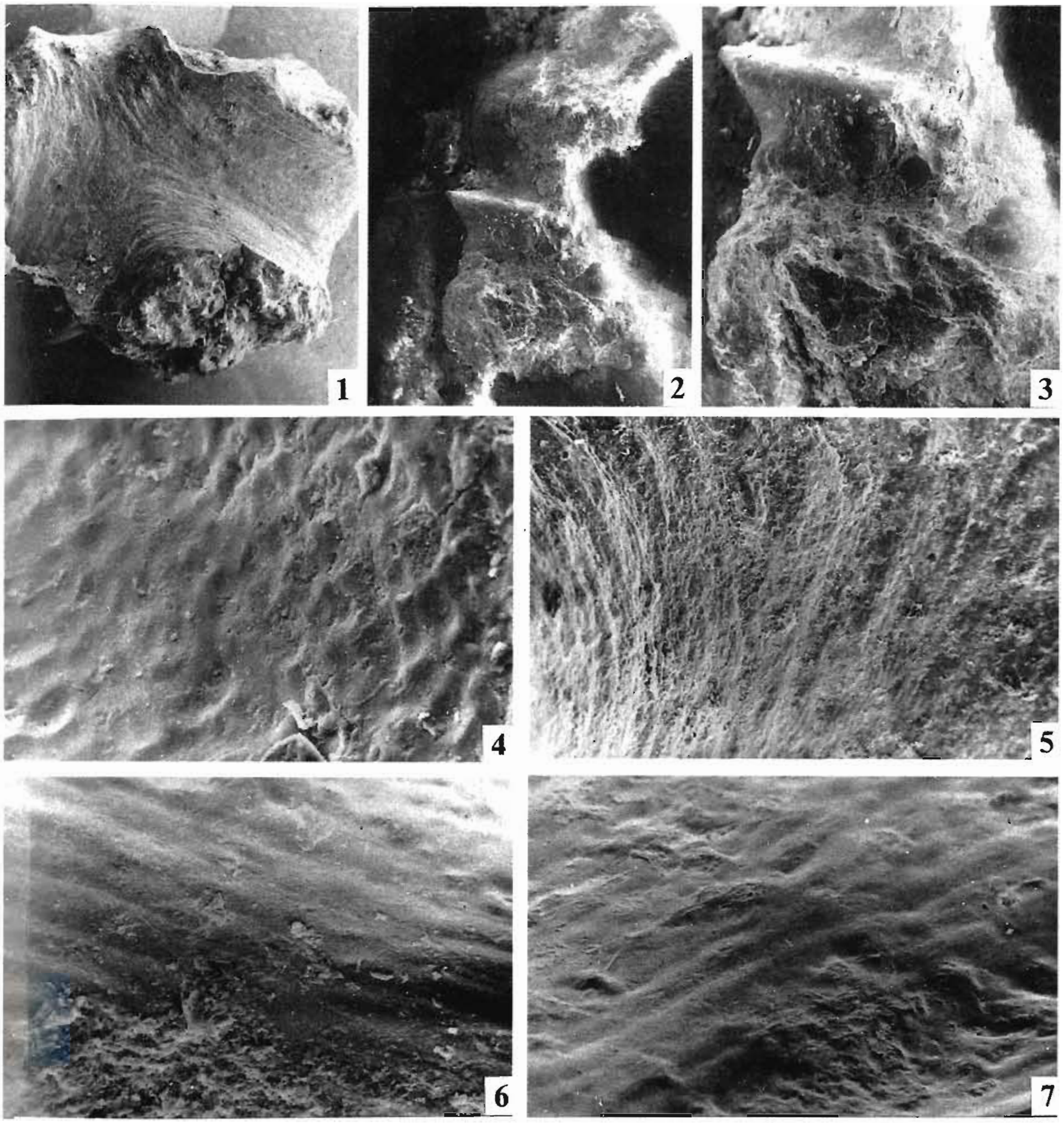

PLATE 4

Peltaspermopsis polyspermis Naug. sp. nov.

Seed-bearing disc and polysperm axes microstructure.

1. Impression of polysperm axis with two seed-bearing disc stalks;
2, 3. Marginal part of seed-bearing disc with two seed scars;
4. Microstructure of seed-bearing disc, adaxial surface;
5-7 Polysperm axis microstructure. Specimen No. 4851/9a (1), 4851/9b (2, 3), 4851/3a (4-7). Zavrajie locality. Magnification: x 10 (1), x 25 (2), x 50 (3, 5), x 250 (4, 6, 7).

Species—**PELTASPERMOPSIS POLYSPERMIS,** sp. nov.
Pl. 1-4.4-8

Diagnosis—Female fructifications are loose racemose aggregates (polysperms) of seed bearing discs (peltoids). Stalks of the peltoids attached to fertile axis in spiral order. The seedbearing disc bears in its central part a depression, which corresponds to position of the stalk attached to the adaxial surface of the disc. The seed bearing discs divided by radial furrows into 20-24 sectors. The seed scars with round outlines, slightly prolonged along radial sectors. The little scarlet of conducting tissues is in the center of seed scar. The margin of seedbearing disc is lobed. The lobes are commonly curved downward (in adaxial direction) and are orientated almost parallel to peltoid stalk.

Sterile leaves are tongue-like or lanceolate, relatively small, with false midvein. The side (secondary) veins curved towards leaf apex.

Description—The studied remains of seed-bearing discs are impressions, which formed as a result of tissue destruction. The sediment matrix conserved "casts" or the outer surface of the fructifications (Fig. 5, 1). Obviously, sediment deposition was very fast and plant remains were deposited before the beginning of the rotting process. A solid iron crust was formed by biogeochemical transformation which was linked with rotting of plant tissues. This crust made possible the conservation of the impressions.

The selected samples include four racemose aggregates (compound polysperms) of seedbearing discs which are preserved to different extents, as well as fifteen fragments and almost complete sterile leaves. The length of polysperm fertile axes is 10-30 mm, but this size is probably only ½ the length of the complete racemose aggregate.

The peltoid stalks are attached to the polysperm axes in loose spiral order (Fig. 6). The basal part of peltoid stalk slightly widens and forms a cone-shaped structure.

Despite the relatively poor preservation of the material (impressions almost without compression) the epidermal characteristics of seedbearing discs were studied by SEM.

The outer microrelief of the epidermis preserved is as negative. The general topography of the cuticle is clearly seen, because cell walls were strongly uplifted under the epidermal surface. Only the microstructure of adaxial surface of the discs with seed scars and the structure of the peltoid stalk were studied.

The main part of adaxial epidermis consists of the isometrical, subrounded cells, sometimes with distinct polygonal outlines (Pl. 3.1, 5, 7; Pl. 4.4). Cell size as a rule is 15 x 20 µm. Slightly bigger cells almost 30 µm in their length occur more rarely. No stomata were found on adaxial surface of the discs. The cells disposed in furrows between disc sectors are more prolonged (Pl. 4.6, 7).

The furrows on the specimens are preserved as ribs (Pl. 4.2, 3). The common size of furrow cells is 15 x 40 µm, sometimes 50 µm in length. The long axes of these cells are orientated along furrows (ribs).

The seed scars are preseved on the impressions as conical- or cupola-shaped protrusions. They consist of loose parenchymatous tissues with unclear cell outlines. The cell walls are slightly curved (Pl. 3.2, 3). The cell size is approximately 10 x 15 µm, i.e., slightly smaller than cells of other parts of adaxial surface of the disc. The seed scar is separated from the sector surface by a distinct line, which apparently corresponds to margins of the scar. The scar often has a narrow

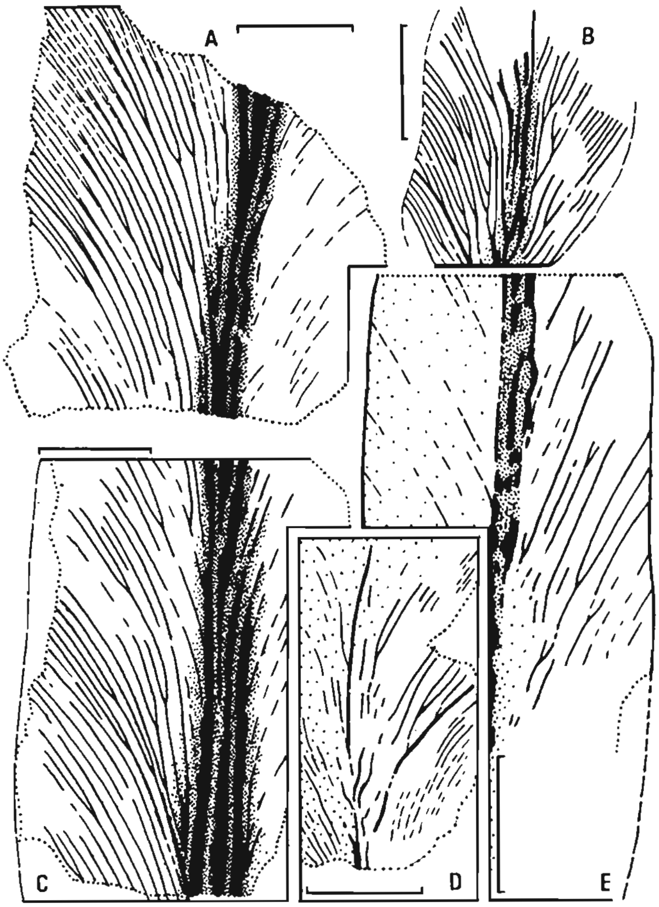

Fig. 7—*Peltaspermopsis polyspermis* Naug. Leaf venation. Zavrajie locality. Scale bar - 1 cm. Specimens: A - 4851/16; B - 4851/15; C - 4851/17; D - 4851/13; E - 4851/14.

marginal limb. Its width is 1/10 of the scar radius. A small protrusion commonly occurs in the central part of the scar, which presumably is the conducting tissue scar.

Not far from the base of the seedbearing disc or at the distal part of peltoid stalk an uncommon microrelief may be seen. This relief is formed by the net of polygonal furrows (Pl. 3.4). The size of the net modules is 20 x 30 µm. These are also probably remains of epidermal cells, but with thicker walls.

Several fragments of stems were found together with the fructifications and sterile leaves of *P. polyspermis*. These stems undoubtedly belong to the same plant, because there are no any other plant remains besides of the stems, peltoids and *Pursongia*-like leaves in the locality. This correlation is also supported by very similar association of *Peltaspermopsis buevichiae* ovuliferous organs and *Tatarina conspicua* leaves, attached to the stems almost identical to the stems found in association with *P. polyspermis* (Gomankov & Meyen, 1986, fig. 28). These stems (Pl. 2.7) are more or less regular cylindrical axes, sometimes slightly narrowing upwards to the supposed stem top. The width of the axes is 11-20 mm. The length

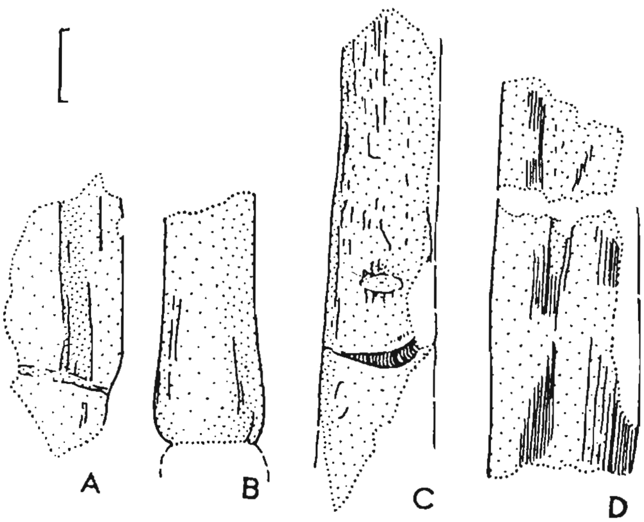

Fig. 8—*Peltaspermopsis polyspermis* Naug. Stems. Zavrajie locality. Scale bar - 1 cm. Specimens: A - 4851/8; B - 4851/4; C - 4851/6; 4851/5.

considerably is more than 10 cm. In cross section the axes are round or ovoid. The ovoid cross-section is secondary and formed by diagenetic compressing of sediment together with the stem.

The stem surface bears elongated folds. Sometimes some rougher and stronger ribs may be observed (Pl. 2.1, 5). In some cases the stem surface may be almost smooth (Pl. 2.2, 6). In addition, there are fine prolonged ribs on the stem surface. These ribs were probably linked with trunk peridermal structure (Pl. 2.3, 4). The rare scars of fallen leaves are sometimes observed. They are elliptical or rhombus-like, elongated across the stem (Fig. 8 C).

One of the important characteristics of these stems is the presence of the nodes (Fig. 8 A-C; Pl. 2.5, 6, marked by arrows), which probably correspond to seasonal interruption of the plant growth.

General morphology of the stems is very similar to young stems of *Ginkgo biloba*, which bear normal leaves arranged in spiral order on the stem when it actively grows, or form a cluster, when the growing is almost stopped during second half of vegetative season (Fig. 9). During winter cold season or extremely hot summer season the leaves were fallen.

The leaves which are associated with generative organs of *P. polyspermis* can be assigned to *Pursongia* Zal. according to formal systematics (see below).

They are relatively small, approximately 5 cm in length. In very rare cases their length is 10 cm. The average width of the leaves is 2 cm. The leaves are entire-margined with parallel margins (Fig. 5 A-C, J), or rarely with gradually narrowing margins from the leaf base to the apex (Fig. 5 E, G). The apex is subtriangular, slightly acute or rounded. The leaf base is also rounded. The venation is fan-shaped or almost pinnate (Fig. 7 A, C, E; Pl. 1.4-6). In the middle part of the leaves the medial cluster of veins is observed. This cluster is formed by several parallel veins, which run together almost up to the leaf apex where they diverge. The cluster itself does not reach the apical 1-1.5 cm. The side (secondary) veins come from the middle cluster at a very acute angle. They commonly dichotomize, first near medial cluster and then closer to leaf margin, forming two or three orders of the side veins. The veins are curved towards the leaf apex. Simple undichotomizing veins also occur. The venation of young scale-like leaves is more complex; the veins may dichotomize four times (Fig. 7, B, D). In some cases such short leaves may have undeveloped basal lobes. Such a lobe has one main vein, which bears dichotomizing side veins.

Etymology —Polyspermis (lat.) – many seeds.

Holotype—GIN RAS, 4851/2.

Occurrence—Salarevskaya Suite, Severodvinsky Horizon, Upper Tatarian, Upper Permian; Russian platform, "Zavrajie" locality.

Discussion—The new species differs from *P. buevichiae* by a big number of the radial sectors, as well as by orientation of the seed scars (the seed scars of *P. polyspermis* are pro-

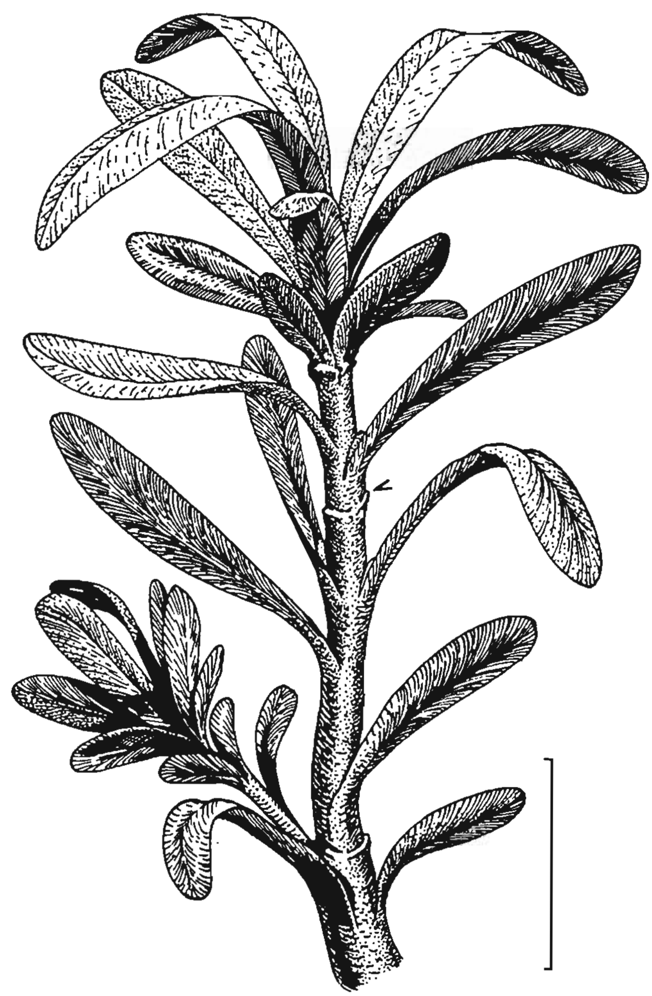

Fig.9— *Peltaspermopsis polyspermis* Naug. Reconstruction of leafy shoot. The season growth interruptions are pointed by arrows. Late Tatarian, West Subangaraland. Scale bar - 10 cm.

longed along sectors) and by the racemose character of the compound polysperms. *P. polyspermis* differs from the *Peltaspermum nanshanense* Durante and *P. multicostatum* Zhang (which were assigned by Durante to *Peltaspermopsis* subgenus) by the smaller size of seedbearing discs in that species and by the racemose character of the polysperms, and also from the *P. nanshanense* by larger number of the radial sectors. The new species is similar to the Lower Permian (Kungurian) *Peltaspermum retensorium* (Naugolnykh & Kerp, 1996) in having a large number of radial sectors. The main difference between these two species is the character of the sterile leaves (leaves of *Peltaspermopsis polyspermis* are simple lanceolate, whereas leaves of *Peltaspermum retensorium* are "fern-like" bi- and tripinnate fronds) and the size of the seed-bearing discs (those of *P. retensorium* are bigger).

An important character of *Peltaspermopsis polyspermis* is seed scar orientation. The scars are prolonged along the radial sectors of the peltoids. By the seed scars position this species clearly differ from the other closely related Upper Permian peltasperms (*P. buevichiae* and *Peltaspermum martinsii*). The seed scars of the last two species are orientated by their long axes across the sectors.

Peltaspermopsis polyspermis is similar to peltoid aggregations from the Kazanian of Pechora Cis-Urals, which were described by Pukhonto & Fefilova (1983) in open nomenclature as *Peltaspermum* sp. "*a*", *P.* sp. "*b*" and *P.* sp. "*c*", by the racemose type of compound polysperms. Sterile leaves associated with *P.* sp. "*a-c*" are still unknown. *Peltaspermopsis polyspermis* differs from the *Peltaspermum* sp."*a*" by the smaller diameter of the discs in beeing three to four times smaller); from *P.* sp. "*b*" and *P.* sp. "*c*" by a considerably larger number of radial sectors; and from the *P.* sp. "c" by the orientation of seed scars, too.

There is quite a big similarity between *Peltaspermopsis* and the compound polysperms associated with *Lepidopteris parvula* Sixtel leaves (Sixtel, 1962) from the Madygenian Suite of Kirgizstan, aged as Middle-Upper Triassic (Dobruskina, 1982). Since the relationship and correlation between these fructifications and leaves *Lepidopteris* may be regarded as proved (Sixtel, 1962), I propose a new combination for the whole plant, *Peltaspermum parvulum* (Sixtel) Naugolnykh, comb. nov. Basionym: *Lepidopteris parvula* Sixtel: Sixtel, 1962, p. 316-319, fig. 9-11, pl. IX, 4-10. Holotype: figured by Sixtel, 1962, pl. IX, 4; spec. 524.

The main difference between *P. parvulum* (Sixtel) Naug. and *Peltaspermopsis polyspermis* is the character of the sterile leaves. The first species has pinnately dissected compound leaves and the latter, simple lanceolate leaves.

The distribution of the taxonomic characteristics among well studied and wide known Permian species of *Peltaspermum* and *Peltaspermopsis,* and also some Triassic peltasperms is shown on Fig. 4.

Genus—PURSONGIA Zalessky, 1933
Species—PURSONGIA AMALITZKII Zalessky 1933
emend. Naugolnykh, emend. nov.
Figs 10; 11 C, D; 12 G (left hand only)

Holotype—figured by Zalessky, 1937, and reproduced here as Fig. 11, C; Upper Tatarian; Russian platform, N. Dvina River, Sokolki locality.

Diagnosis—The sterile leaves with lanceolate outlines, sometimes shortened, scale-like, ovoid or subtriangular. The proportion between width and length is approximately 1/5-1/6. The leaf margin are entire, gradually gathering towards the leaf apex and base. In the middle part of developed leaf the margins are parallel to each other. The false midvein (vein cluster) consists of several strands of vascular tissue. The side (secondary) veins come from the middle cluster. The side veins are simple or rarely 2-3 times dichotomizing. The side veins are arch-like curved and strongly decurrent along the false midvein.

Description—The general leaf morphology of this species is defined by position of maximal leaf width. As a rule, the maximal width is located at lower part of the leaf lamina, or even near the leaf base (Figs 10 C, left; D, F; 10 A, F, 11). Sometimes uncommon aberrant specimens also occur. Their maximal width is in the middle or upper part of the leaf (Fig. 10 G, H). It is interesting to note that the opinion about superficial similarity between macromorphology of *P. amalitzkii* and some Gondwana glossopterids (*Glossopteris crenulata* Brongn., *G. indica* Schimper) appeared after studying such aberrant specimens.

There is no leaf in my collection which bears a completely preserved base. The most complete fragments (Fig. 9 A, G, H) give us sufficient grounds to assume that the leaf base was wedge-like.

The false midvein of our specimens corresponds to shallow furrows (if the leaf is orientated to observer by its adaxial surface) or ribs (if the abaxial surface). The width of false midvein varies from 2-25 mm near leaf base to 05-1 mm near apex. The side veins are very thin and fine, feebly impressed in matrix. They are seen only in indirect light.

In the protologue of *P. amalitzkii,* the author of the species Zalessky noted the presence of anastomoses between the side veins. Such anastomoses (very rare and unclear ones) were shown on Zalessky's figures (see Fig. 11 C, D here). However, our specimens from the type locality "Sokolki" of *P. amalitzki* (i.e., topotypes) do not bear any anastomoses-like structures.

Comparison – *P. amalitzkii* differs from the other related species of *Pursongia* – *P. beloussovae* (Radcz.) Gom. & Meyen, *P. elegans* Durante – by considerably bigger leaves. *P. amalitzkii* differs from *P. serrata* (Srebrod.) Meyen by the entire leaf margin.

Remarks – Leaves which probably belonged to

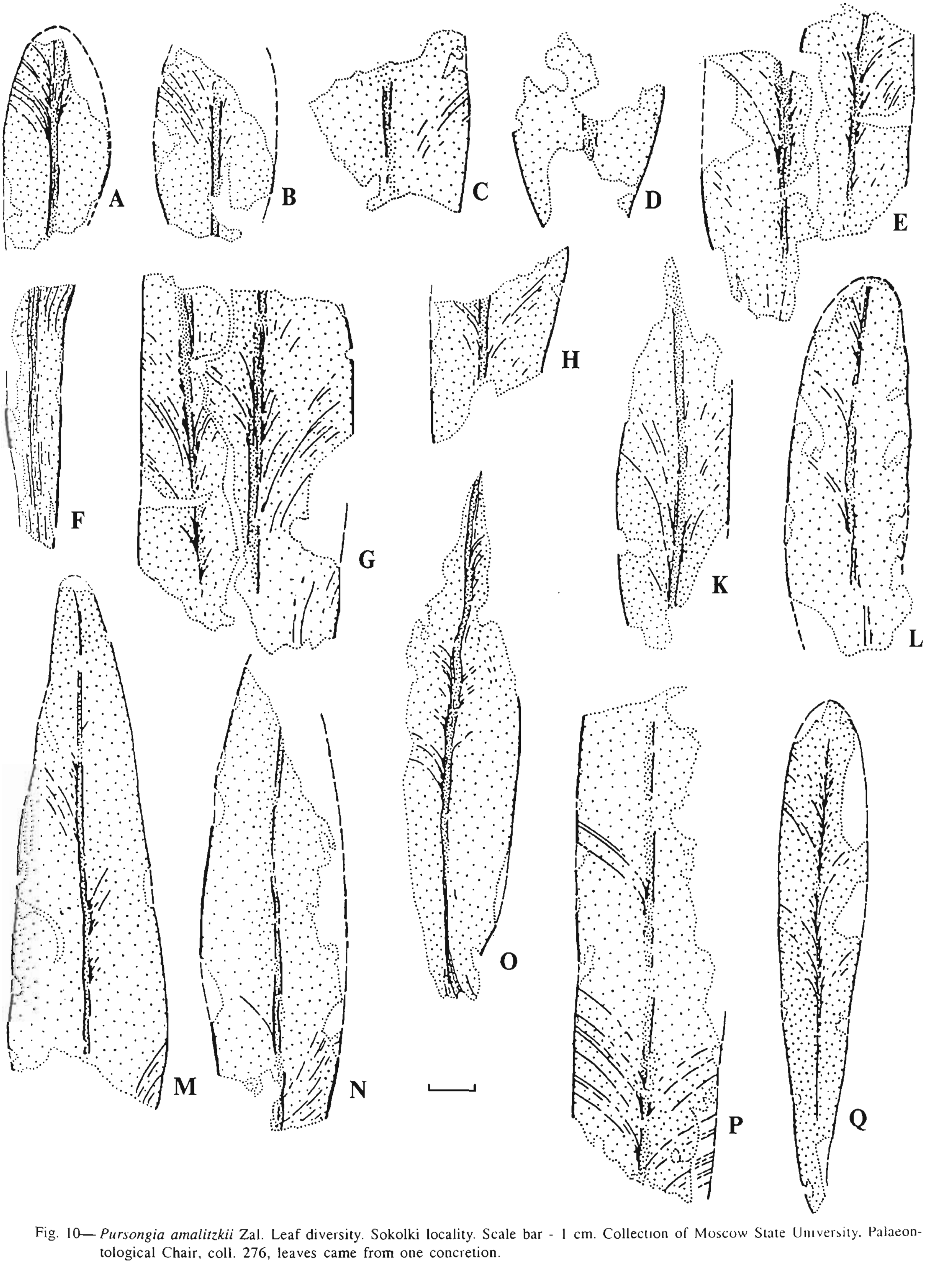

Fig. 10— *Pursongia amalitzkii* Zal. Leaf diversity. Sokolki locality. Scale bar - 1 cm. Collection of Moscow State University, Palaeontological Chair, coll. 276, leaves came from one concretion.

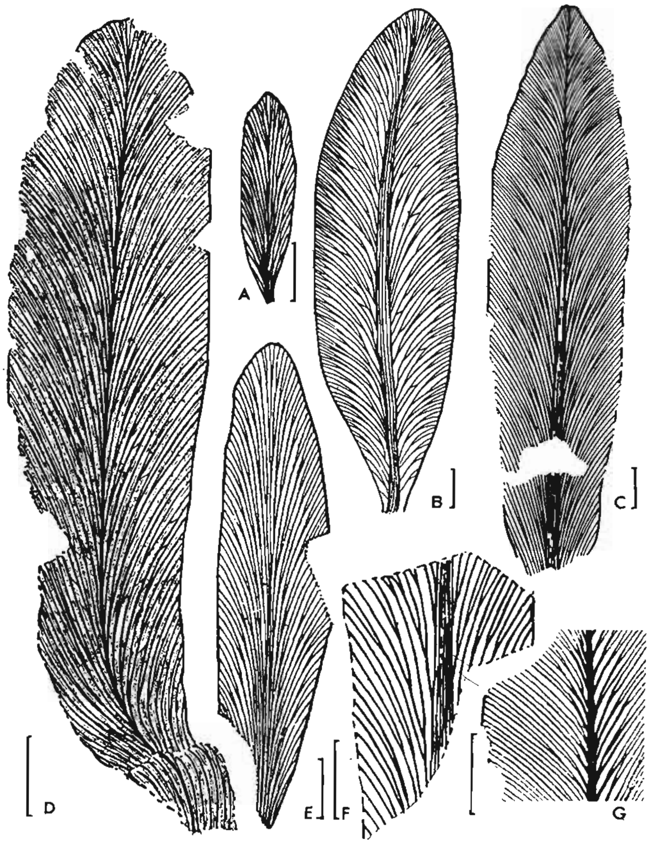

Fig. 11— *Pursongia* and leaves of some related taxa from the Upper Permian of Eurasia, after Zalessky, 1934, 1937 A, E - *Petcheria elongata* Zal., B - *Pursongia asiatica* Zal., C, D - *P. amalitzkii* Zal., F - *Pereborites rarinervis* Zal., G - *Compsopteris tchirkovae* Zal. (this figure is given for comparison, since separated pinnules of this pteridosperm and some related genera similar to *Pursongia*, but differ by the presence of true midvein). Localities: Kuzbass, Ishanovo village (B), Pechora coal basin: Pechora River (A, E), Perebor River (F), Big Synia River (G), Russian platform, Northern Dvina River, Sokolki locality (C), South Cis-Urals, Sakmara River, Kolgumkino village (D). Upper Permian. Scale bar - 1 cm.

Pursongia were described for the first time by Fischer von Waldheim (1840) from the Upper Permian (Tatarian?) of the Orenburg region (Southern Urals). They were assigned by him to some species of *Glossopteris: G. phillipsii* Brongn., *G. crenulata* Brongn. A few years later the last species was noted by Mercklin (1852) from the Upper Permian deposits, presumably of the northern part of Russia.

After half a century the first representative collection of Upper Permian plant remains was obtained by Amalitzky from the Upper Tatarian of Severnaya Dvina Basin. Initially Amalitzky determined a number of typically Gondwanan elements in his possession obviously under the influence of Fischer von Waldheim and Mercklin's papers: *Glossopteris angustifolia* Feistmantel, *G. indica* Schimper, *G. stricta* Bunb., *Gangamopteris cyclopteroides* Feistmantel, *G. major* Feistmantel (Amalitzky, 1901).

The presence of typical Gondwana glossopterid taxa in Amalitzky's localities was in good agreement with the Upper Permian tetrapod fauna of N. Dvina, which was related to the famous South Africa Karroo fauna. Nevertheless, Zalessky restudied Amalitzky's collection a few years later and described similar leaves from the Upper Permian (Upper Kazanian and Tatarian) deposits of Tatarstan under new generic and species names *Pursongia amalitzkii* Zal. (Zalessky, 1929, 1933).

According to Zalessky, the new genus *Pursongia* differs from *Glossopteris* by the presence of hypodermal tissue strands between the side veins. Zalessky thougth that *Pursongia* had anastomoses and net-venation. The genus *Pursongia* with type-species *P. amalitzkii* and some closely related species, *P. angustifolia* Zal. and *P. asiatica*, were assigned by Zalessky to the order Glossopteridales.

Neuburg (1948) noted during redescription of *P. asiatica* Zal. from the Permian deposits of Kuzbass that she could not find anastomoses and hypodermal tissues between side veins. Despite her scepticism about the genus validity, in subsequent works (Neuburg, 1954; Bobrov & Neuburg, 1957) she used this genus widely and even described several new species: *Pursongia tunguscana* Neub., *P. mongolica* Neub. and proposed new combination *P. uralica* (Zal.) Neub. The last species was initially established by Zalessky on a single specimen of leaf fragment from the Kungurian of the Middle Fore-

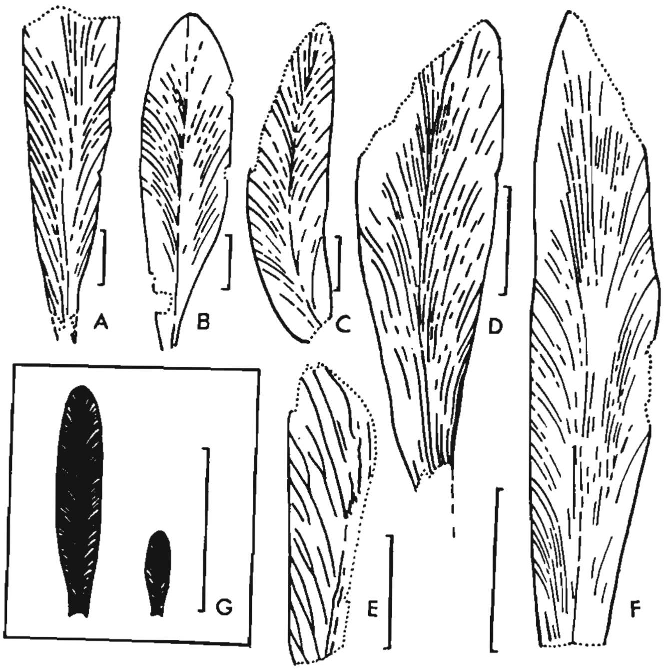

Fig. 12—*Pursongia* and some similar leaves from the Upper Permian of Pechora basin. A-D - *Pursongia* sp., E - *Rossovites* cf. *petschorensis* Zal., F - *Zamiopteris* sp. Pechora Cis-Urals, Yangarey River (A), Paemboy Coal Mines, Talbeyskaya Suite (B-F). G - relationship between middle size leaves of *Pursongia amalitzkii* Zal. (left) and *Pursongia* sp. ex Pukhonto et Fefilova (right). A-F - after Pukhonto, Fefilova, 1983. Scale bar - 1 cm (A-F) and 10 cm (G).

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taeniopteris Brongniart, 1828	+	+	-	-	-	-	+	?	+	-	-	-	+	-	-	+	[illegible]	-
Rhubidgea Tate, 1867	+	-	-	-	+	?	+	-	-	-	+	+	-	-	+	-	-	-
Zamiopteris Schmalhausen, 1873	+	-	-	+	+	-	+	-	-	-	+	+	-	-	-	-	+	+
Palaeovittaria Feistmantel, 1876	+	-	+	-	+	-	+	?	-	-	+	-	+	-	+	-	+	-
Euryphyllum Feistmantel, 1879	+	-	-	-	?	+	+	-	-	-	+	+	-	-	+	-	-	-
Lesleya Lesquereux, 1880	+	-	?	-	+	-	+	-	-	-	+	+	-	-	-	-	+	-
Strzeleckia Johnstone, 1896	+	-	-	+	?	+	+	-	+	-	-	+	-	-	-	-	+	-
Protophyllocladus Berry, 1903	-	-	+	-	-	-	+	?	-	-	+	-	+	+	-	-	+	-
Glottophyllum Zalessky, 1912	+	-	-	+	+	-	-	+	+	-	-	+	-	-	-	-	+	-
Linguifolium Arber, 1913	+	+	-	-	-	-	+	-	-	-	+	+	-	-	+	-	?	-
Scapanophyllum Zalessky, 1929	+	-	-	+	+	-	+	-	-	+	-	+	-	-	-	-	+	-
Tychtopteris Zalessky, 1930	-	-	-	+	+	-	-	+	+	-	-	+	-	+	-	-	+	-
Pursongia Zalessky, 1933	+	-	-	+	+	-	+	-	+	-	-	+	-	-	-	-	+	-
Petcheria Zalessky, 1933	+	-	-	+	+	-	-	+	+	-	-	+	-	-	+	-	-	-
Listrophyllum Zalessky, 1934	+	+	-	-	-	-	-	+	-	-	+	+	-	-	-	-	+	-
Velisia Frenguelli, 1941	+	+	-	-	-	-	+	-	-	-	+	+	-	-	-	-	+	-
Phyllopteroies Medwell, 1954	-	+	-	-	-	-	+	-	-	-	+	+	-	+	-	-	+	-
Evenkiella Radczenko, 1960	+	-	-	+	-	+	+	-	?	-	?	-	+	-	+	-	-	-

Fig. 13—The main characters of *Pursongia* and some related leaf genera: 1 – Leaf is simple, entire margined or slightly lobed, 2 – True midvein runs from leaf base to apex, 3 – True midvein is evident only in leaf base, 4 – True midvein is absent, 5 – Vein cluster (false midvein) is present, 6 – Fan-shaped venation, 7 – Wedge-like base, 8 – Stalk is present, 9 – Apex is rounded, 10 – Apex is emarginate, 11 – Apex is acute, 12 – Side (or margin) veins are several times (up to 4) dichotomizing, 13 – Side (or margin) veins are simple as a rule, 14 – Developed side lobes are present, 15 – Side veins run at very acute angle to leaf axis (20-30°), 16 – Side veins run at almost 90°, 17 – The angle of side veins is diverse (30-80°), 18 – Epidermal pattern is known for some species. The genera *Paratatarina* Vassilevsk., *Uralophyllum* Kryschtof. & Prynada, *Maria* Dobrusk., *Glosophyllum* Krausel, *Rhabdotenia* Pant are absent in this table because diagnoses of these genera based on epidermal-cuticular characters.

Urals and first assigned to *Glossopteris*.

Rasskasova (1960) analyzed the composition of *Pursongia*, which contains six species: *P. amalitzkii* Zal., *P. angustifolia* Zal., *P. asiatica* Zal., *P. tunguscana* Neub., *P. mongolica* Neub., *P. uralica* (Zal.) Neub. All of these species originated from the uppermost Lower Permian and Upper Permian of Russian platform and Siberia. She concluded that the genus was heterogeneous and included species with quite different macromorphology. Rasskasova established new monotypical genus *Czapcoctia* Rassk. from the Upper Permian (Peljatkinskaya Suite) of Tunguska Basin. The single specimen (holotype) of *C. magnifolia* was an impression of the middle part of simple lanceolate leaf with pinnate venation. The rare anastomoses were observed. The peculiarity of the described leaf does not raise doubts about the validity of the genus *Czapcoctia*. However, substantiation of the genus established in the protologue was insufficient because the diagnostic features by which *Czapcoctia* differs from *Glossopteris* were not mentioned. In my opinion, the presence of well-developed real midvein and very dense generally pinnate venation may be regarded as such characteristics.

Besides, Rasskasova described new specimens of *Pursongia tunguscana* Neub. in the same paper. These specimens originated from the Upper Permian of Siberia (Iljinskaya Suite of Kuzbass and Peljatkinskaya Suite of Tunguska Basin). The anastomozing of the side veins is very well shown on Rasskasova's photographs and figures. These leaves fully comply with the diagnosis of *Glossopteris*.

After studying Kuzbass species of *Pursongia*, Betekhtina (1965) referred them to three main types of their venation: (1) false glossopteroid venation – *P. uralica* (Zal.) Neub., (2) semi-looped venation – *P. tunguscana* Neub., (3) net-looped venation – *P. mongolica* Neub. According to Betekhtina, the anastomoses are characteristic for all three types of venation. The presence of true anastomoses for Kuzbass leaves assigned by Betekhtina to earlier established species *P. mongolica, P. tunguscana* and *P. uralica* f. *nana* Betekhtina was convincingly documented with the help of good photographs (Betekhtina, 1965, Pl. 2). The leaves of *Pursongia* species without anastomoses in Betekhtina's paper were not discussed.

The presence of real net-venated leaves in Angaran Permian floras was proved by Zimina (1967), who described new species *Glossopteris orientalis* Zim., *Gangamopteris ussuriensis* Zim. and *G. pacifica* Zim. from the Upper Permian of Russian Far-East (Primorie). The floristic assemblage is characterized by generally Angaran taxonomic components. As a possible migration way of glossopterids Zimina pointed Monglia where glossopterids from the Upper Permian deposits are also known. The new combinations *Glossopteris tunguscana* (Neub.) Zim. and *G. mongolica* (Neub.) Zim. were proposed in the same paper.

The revision of *Pursongia* and plants, which were unjustly assigned to this genus, was impossible for a long time because there were no data about type-species *P. amalitzkii*. The material that I have in my possession let to suggest the main principles of such a revision. The species *P. amalitzkii* (including possible young synonym *P. angustifolia* Zal.), *P. asiatica* Zal., *P. beloussovae* (Radcz.) Gom. & Meyen, *P. elegans* Durante and related species without anastomoses between side veins should be assigned to the genus *Pursongia*. The species *Glossopteris orientalis*, *G. tunguscana*, *G. mongolica* (two last species were formerly described as *Pursongia*) may be assigned to genus *Glossopteris* according to its formal diagnosis, despite the fact that these Angaran leaves may not necessarily belong to the order Glossopteridales (Dictyopteridales sensu McLoughlin, 1990, 1995).

A number of genera related to *Pursongia* Zal. by their morphology are known from the Upper Palaeozoic of Angaraland. They are *Listrophyllum* Zal., *Glottophyllum* Zal., *Zamiopteris* Schmalh., *Petcheria* Zal., *Evenkiella* Radcz., *Scapanophyllum* Zal., *Tychtopteris* Zal. They differ from *Pursongia* by the presence of the following characteristics: (1) well developed midvein (*Listrophyllum*), (2) developed stalk (*Listrophyllum, Glottophyllum, Tychtopteris*, partly some species of *Petcheria*), (3) bifurcated apex (*Scapanophyllum*), (4) developed side lobes (*Tychtopteris*).

It is more difficult to formalize the boundary between *Pursongia* and *Zamiopteris*. There are certain distinctions between the epidermal structure of *Tatarina* Meyen (nomenclatorial variant of *Pursongia* for the species with known epidermal-cuticular structure) and some species of *Zamiopteris* (*Z. neuburgiana* Meyen, *Zamiopteris* sp. ex Meyen, 1969) with known microstructural characteristics. This difference does not allow to suggest that *Zamiopteris* and *Pursongia* are synonyms. However, macromorphologically these genera are very similar. The formal distinctions between *Pursongia* and *Zamiopteris* are stronger venation of representatives of the last genus and, as a rule, their acute apices (the apex of *Pursongia* leaves is commonly round).

A younger synonym of *Pursongia* is *Tersiella* Radcz. as is already noted (Gomankov & Meyen, 1986).

Another undoubted synonym of *Pursongia* is *Pereborites* Zal., which was later redescribed by Pukhonto (in: Pukhonto & Fefilova, 1983). Unfortunately, in the description of this genus, Pukhonto did not point out the species composition, though she referred to another species apart from the type-species of *Pereborites*. The comparison with other genera is also absent. In the same work, Pukhonto wrote about the presence of the midvein of *Pereborites*. Judging from the figured holotype (seen here as Fig. 11 F) as well as from Pukhonto's specimens, this latter opinion is obviously mistaken. The incorrect nomenclatorial actions for the choice of lectotype and the reference to neotype (different specimens are taken as neotype) devalue Pukhonto's attempt to modify the diagnosis of *Pereborites* genus and to make it valid.

Evenkiella differs from *Pursongia* by the absence of a midcluster of veins (false midvein) and possibly belongs to *Cordaites*-like plants.

Fig. 13 shows the distribution of characteristics between *Pursongia* and other genera, which are used for simple lanceolate leaves *Lesleya* Lesquereux, *Linguifolium* Arber emend Retallack, *Palaeovittaria* Feistmantel and others.

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