Wulfenia **27** (2020): 97–113

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

# *Archaeopetalanthus progressus* gen. et sp. nov. – a new representative of the vojnovskyopsid gymnosperms from the Carboniferous of Siberia (Russia)

Serge V. Naugolnykh

*Summary:* A new representative of the vojnovskyopsid gymnosperms is described on the basis of the fertile material from the Middle to Upper Carboniferous of Siberia, Russia. A new genus and species *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. are established. The new plant is characterized by having bisexual reproductive organs (strobili) of obconic shape, with numerous sterile scales disposed around the abaxial area of the strobilus, small round to ovoid microsporangia disposed on the abaxial surface of the strobilus, possible glands between the microsporangia and the bases of the sterile scales and long seed stalks located between the scales and bearing seeds of *Samaropsis*-type. History of study of vojnovskyopsid gymnosperms and the key points of systematics of this plant group are discussed.

*Keywords:* gymnosperms, Vojnovskyales, Vojnovskyopsida, paleobotany, Carboniferous, Siberia, reproductive organs, new taxon

The Carboniferous and Permian continental deposits of Angaraland (North-Eastern regions of Russia and adjacent areas) are well-known for including numerous lanceolate leaves of gymnosperm affinity, which are often cited as cordait-like leaves or even as leaves of so-called 'Angaran cordaits' (Radczenko 1961; Neuburg 1965; Meyen 1982, 1984, 1987). Despite their superficial similarity with the leaves of true European or North American cordaits (the order Cordaitales), the Angaran *Cordaites*-like leaves belonged to a considerably different plant group, i.e. the order Vojnovskyales. The Vojnovskyales order is of such high morphological peculiarity among the Late Palaeozoic gymnosperms that it should be separated into a special class Vojnovskyopsida (Naugolnykh 2010), related to the sister class Pinopsida.

The vojnovskyans appeared as plant group in vegetation history suddenly and only little is known about their origin. The monotype genus *Hissarocarpophyllum* L. Savizkaja can be considered as a possible ancestor of the vojnovskyopsids, with the type species *H. lyratum* L. Savizkaja (Savitskaja 1970) from the Lower Carboniferous of Central Asia (the Hissar Ridge; another transliteration is Gissar Ridge; Uzbekistan).

Savitskaja (1970) compared the genus *Hissarocarpophyllum* with the morphologically similar genera *Niazonaria* Radczenko and *Taibia* Zalessky. The strobiloid reproductive organs of *Hissarocarpophyllum* are also similar to the shortened, 'dorso-ventrally' flattened morphs of the cones of *Vojnovskya* Neuburg (Neuburg 1965: Plate XXXI, fig. 3), some specimens of the female reproductive organs *Astrogaussia* Naugolnykh (2014) and representatives of the genus *Scirostrobus* Doweld et Naugolnykh (Doweld & Naugolnykh 2002), closely related to *Astrogaussia*.

The winged seeds of somewhat asymmetrical shape described as *Protopityospermum monoptericum* L. Savizkaja in the same paper (Savitskaja 1970) were found together with the reproductive organs of *Hissarocarpophyllum lyratum*, but not in natural connection to the strobili. Savitskaja (1970) did not mention a similarity between these seeds and the typically Angaran genus

*Sylvella* Zalessky, which most probably also belonged to the vojnovskyopsids (Meyen 1984, 1987). Nonetheless, Savitskaja noted some features in common between *Protopityospermum monoptericum* and the seeds *Pityospermum* (?) *dubium* Neuburg from the Lower Permian deposits of the Kuznetsk Basin, Siberia (Neuburg 1948). The latter species is very close to the typical representatives of *Sylvella.*

As it was already briefly mentioned above, the vojnovskyopsids are often cited in paleobotanical literature as so-called 'Angaran cordaits' or even just as 'cordaits', but actually the structure of their reproductive organs are too uncommon and could not be explained in terms of classic morphology of the male or female cordaitalean cones or cones of the pinopsids in general. Obviously, this peculiar and uncommon morphology did not allow to understand the structure of the vojnovskyopsid reproductive organs for a long time and did not allow to clarify their links with the *Cordaites*-like leaves from the Upper Palaeozoic of Angaraland. The great event in history of study of the 'Angaran cordaits' was the publishing of the Meyen's work (1982) focused on the description of the reproductive organs *Kuznetskia tomiensis* Gorelova et S. Meyen, *K. planiuscula* S. Meyen and *Pechorostrobus bogovii* S. Meyen in a broad connotation with the problem of 'Angaran cordaits'. Further studies by Meyen (1984, 1987, 1988) and his students made it possible to get new information about reproductive organs of vojnovskyopsids and related taxa (Ignatiev 1988, 2001, 2011; Ignatiev & Meyen 1989). Gymnosperms of putative vojnovskyopsid affinity were found even in the Permian deposits of North America (Rothwell et al. 1996).

According to the viewpoint of the present author, the vojnovskyopids are gymnosperms with female reproductive organs, which are represented by racemose aggregations of winged platyspermic seeds attached to long or short seed stalk attached to the fertile axis in loose or compact spiral order. Male reproductive organs consist of a long axis, sometimes apically wide, bearing microsporangia (pollen sacs) arranged on the axis in spiral order. Bisexual reproductive organs also occur. Lower and middle parts of both female and male reproductive organs could possess sterile scales.

## Brief history of study of vojnovskyopsid gymnosperms

One of the earliest records of the reproductive organs belonging to vojnovskyopsids was published by the outstanding Russian paleobotanist Zalessky (1934). This organ was described as new genus and species *Taibia tyrganensis* Zalessky. The specimen originated from the Permian deposits of the Promezhutochnaya Suite (Intermediate Formation) of the Kuznetsk Basin. Three years later, Zalessky described one more species of the same genus, i.e. *T. insigne* (original spelling of the specific epithet) Zalessky from the vicinity of the City of Prokopievsk, the coal-bearing layer Lutuginsky (Zalessky 1937).

Neuburg (1948), who reproduced images of *Taibia* published by Zalessky, expressed an opinion that both species are close to the genus *Gaussia* Neuburg (nom. illeg.; now *Astrogaussia* Naugolnykh), and especially to the species '*Gaussia*' *scutellata* Neuburg. But in my view, this opinion is not appropriate, and it is much more likely that at least the specimen described by Zalessky as *Taibia insigne* (or *insignis* according to Neuburg) is much more similar to the apical part of the reproductive organ of *Vojnovskya* bearing long linear sterile scales.

Nonetheless, one of the specimens attributed by Zalessky to *Taibia tyrganensis* (see for images: Zalessky 1937: 138, fig. 21; Neuburg 1948: Plate LXXI, fig. 8) actually resembles '*Gaussia*'

*scutellata* and it is even more similar to the species *Astrogaussia imbricata* (Naugolnykh) Naugolnykh (Naugolnykh 2014). But another specimen attributed to the species *Taibia tyrganensis* by both Zalessky and Neuburg (see for image: Neuburg 1948: Plate LXXII, fig. 9) is much more similar to the isolated seed-bearing megasporophyllous disc (peltoid) of peltaspermalean affinity. The sterile leaves of peltasperms (*Permocallipteris* spp.) occur in the same deposits.

The genera *Niazonaria* Radczenko (Radczenko 1933) and former '*Gaussia*' Neuburg were interpreted by Neuburg (1934, 1948) as microsporangiate/male fructifications or aggregations of microsporophylls. In contrast to this opinion, Krassilov & Burago (1981) and Meyen (1982, 1987, etc.) believed that the genus *Gaussia* Neuburg was established on female reproductive organs. The present author joined the same opinion on the basis of studied material from the Lower Permian floras of the Urals (Naugolnykh 2014).

Concerning the gender nature of the reproductive organs of *Vojnovskya* Neuburg, the viewpoints of paleobotanists diverge considerably. When the genus *Vojnovskya* was initially described (Neuburg 1965), it was interpreted as bisexual. Obviously, the same interpretation was shared by Zimina (1967) and Sixtel et al. (1975), but the latter scientists did not discuss the gender nature of *Vojnovskya* in detail.

Meyen (1982, 1987) firmly considered *Vojnovskya* as a female reproductive organ. The same opinion was supported by the present author as well (Naugolnykh 2001), till the numerous monosaccate pollen grains were extracted by me from the *Vojnovskya*-like reproductive organ found in the Lower Permian (the Kozhimrudnitskaya Formation) deposits, outcropped on the left bank of the Kozhim River, 3 km downstream from the Kozhim-Rudnik station (the outcrop 2012, Komi Republic, Pechora coal basin, Russia; see for details: Naugolnykh 2010). Pollen was obtained from the funnel-shaped depression disposed in the central area of the abaxial surface of the reproductive organ filled by a bright coaly matter (possible remnants of small microsporangia). Pollen grains are small, ovoid to round, 16×19 µm of average dimension, anasulcate, similar to pollen of recent Araucariaceae. Most probably, the microsporangia were not adult.

These pollen grains are practically identical to pollen extracted by Meyen from the microsporangia of *Pechorostrobus bogovii* S. Meyen (Meyen 1990: Plate XLIV, figs 5, 10, 11; Plate XLV, fig. 3) and also similar to the dispersed pollen grains found on the spermoderm of the seeds *Bardocarpus discretus* (Neuburg) Neuburg (Meyen 1990: Plate XLV, figs. 7, 8).

All data, which were published later and which are beyond of the scope of the present study, together with the new incoming discoveries of the reproductive organs of vojnovskyopsid affinity unequivocally show that the general comprehensive picture of morphological diversity of vojnovskyopsids is far away from its final form. I try to avoid discussing here some doubtful finds, which need additional and very careful restudy and redescription. The main aim of the present work is to describe a new type of vojnovskyopsid reproductive organs with bisexual nature.

## Materials and methods

The material under study was collected from the Listvjanskaya Formation from Middle to Late Carboniferous. The material was provided to the present author by the geologist V.E. Sivchikov, whom I express my deep and sincere gratitude. The locality is disposed on the right bank of the Kan River, in mouth part of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk, the Kansk District of the Krasnojarsk region, Siberia, Russia.

The material is represented by a single sample containing plant remains (reproductive organs, seeds and leaves, most probably belonging to one and the same parent plant). The plant fossils are imprints with small amount of impressed coalified material. The coaly parts of microsporangia were macerated in nitric acid for a week. The obtained pollen grains were studied in optic microscope PZO with interference contrast.

The specimen studied is kept at the State Darwin Museum (abbreviated name cited below: SDM), Moscow, under number 4846/153.

## Systematics and description

Division **Pinophyta Reveal, 1996**

Classis **Vojnovskyopsida Naugolnykh, 2010**

Order **Vojnovskyales Neuburg ex Emberger, 1968**

Family **Vojnovskyaceae Neuburg, 1963**

### *Archaeopetalanthus* Naugolnykh, gen. nov.

**Etymology.** Archaeo – old (Latinized Greek); petalus (Latin) – petal; anthus (Latinized Greek) – flower, blossom.

**Type species.** *Archaeopetalanthus progressus* Naugolnykh, sp. nov., Middle to Upper Carboniferous of Siberia.

**Diagnosis.** Same as for the type species.

**Comparison.** The most morphologically similar to *Archaeopetalanthus*, but geologically younger genus is *Astrogaussia* Naugolnykh, 2014 (former *Gaussia* Neuburg [p.p.] non H.A. Wendland, 1865 (Wendland 1865)). The main difference is the bisexual type of *Archaeopetalanthus* in contrast to the strict female nature of *Astrogaussia*. Both genera *Archaeopetalanthus* and *Astrogaussia* are different from the genus *Paravojnovskya* Doweld, 2004 (Doweld 2004) in its narrow sense (discussion see in: Naugolnykh 2014) in the presence of well-developed linear or lanceolate sterile appendages (bracts) and mutually free arrangement of both bracts and seed stalks.

One more similar genus is *Krylovia* Chachlov, 1939 (= *Samarospadix* Neuburg, 1948) from Middle and Upper Carboniferous of Angaraland. According to the diagnosis of the genus *Krylovia* given by Ignatiev (2001), the cones (strobili) of this genus did not have any sterile appendage, what is a considerable difference between *Krylovia* and *Archaeopetalanthus*. Stratigraphically, the original material of *Krylova sibirica* Chaclov came from the similar strata as *Archaeopetalanthus*, i.e. Middle to Upper Carboniferous, the Alykaevskian Horizon; type locality is the Mostochki ravine near Staraya Balakhonka Village, Kuzbass (Ignatiev 2001). The seeds found in natural connection with the reproductive organs of *Krylova sibirica* (Ignatiev 2001: 105, fig. 1) are basically similar to the seeds of *Archaeopetalanthus progressus*, although seeds of *Krylovia* show higher variability in size, as it is demonstrated on the reconstruction of *Krylovia sibirica* proposed by Ignatiev (2001: 107, fig. 3).

There are some features in common between *Archaeopetalanthus* and *Vojnovskya* Neuburg, 1965, but the latter genus was reinterpreted as male reproductive organs (Naugolnykh 2010). Nonetheless, type of the pollen produced by *Archaeopetalanthus* and *Vojnovskya* is one and the

same, i.e. small (16–30 µm in diameter on average), anasulcate with smooth to finely scabrate surface.

**Distribution.** Middle and Upper Carboniferous of Siberia.

***Archaeopetalanthus progressus* Naugolnykh, sp. nov. (Figs 1A–C, F; 2A–C; 3A–C; 4A–F; 5A–F; 6A–B; 7A–D, F, G; 8A–D, F, G; 9)**

**Etymology.** Progressus (Latin) – evolutionary advanced.

**Holotype.** SDM No 4846/153-A; the Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk.

**Diagnosis.** Bisexual reproductive organs consist of an axis of obconic shape, with narrow base and widening upper part. Central part/central area of upper (abaxial) surface of the axis bears numerous microsporangia producing anasulcate pollen. Peripheral margins of abaxial surface bear radially orientated long and narrow appendages. Most of appendages sterile. Some of appendages have terminal winged seeds. Small glands between microsporangia and basal parts of appendages.

**Description.** The single, although well-preserved, specimen (Fig. 1A), which is subject of the present study, includes four rosette-like reproductive organs obviously belonging to one and the same parent plant, most probably even to one individual plant organism. The reproductive organs are preserved separately, without clear attachment to the common branch. These rosette-like organs are visible from different sides and in different positions. The most representative organ, which was selected as the holotype (4846/153-A), is observed from its upper surface (Fig 1F). Others are diagenetically deformed and flattened along the main axis, and thus these organs are seen laterally (Figs 3A; 4F; 5C; 7B).

Each individual organ consists of an axis of obconic shape, with the narrow or even wedge-like basis and a widened upper part. Size of the apical part (abaxial area of the reproductive organ) varies from 1–2 cm, length of the axis, as far as we can judge from the material in hand, is about 1–1.5 cm. The surface of the upper part (abaxial surface) of the axis has a round shape and is covered by numerous round to ovoid bodies (Figs 3A, C; 4F). Number of the bodies varies from forty to sixty. Maceration of the bodies allowed to obtain several anasulcate pollen grains (Figs 1A, B; 4A–E), some of which were aggregated into tetrads (Figs 1B; 4A). Surface of pollen is micro-scabrate. Average size of pollen is about 25–30 µm. The presence of pollen grains inside the round or ovoid bodies unequivocally shows that these bodies are microsporangia. Average size of the microsporangia is 0.5–1 mm in maximum. The best preserved microsporangia demonstrate an apical split adapted for releasing of pollen, when the microsporangia became adult and ready for dispersing pollen. There is a small black coaly spot disposed exactly at the center of the apical area of the axis. Obviously this spot corresponds to the central conductive strand located in the axis of the organ.

The round apical area of the axis (abaxial part of the cone) is surrounded by long and narrow petal-like appendages, radially arranged in relation to the central part of the upper surface of the axis. Most of the appendages are sterile, but some of them (at least three per rosette-like organ, or maybe slightly more) bear the terminally disposed winged seeds. Length of the appendages is more or less equal and is about 8–9 mm; the width varies from 0.5 mm to 1 mm.

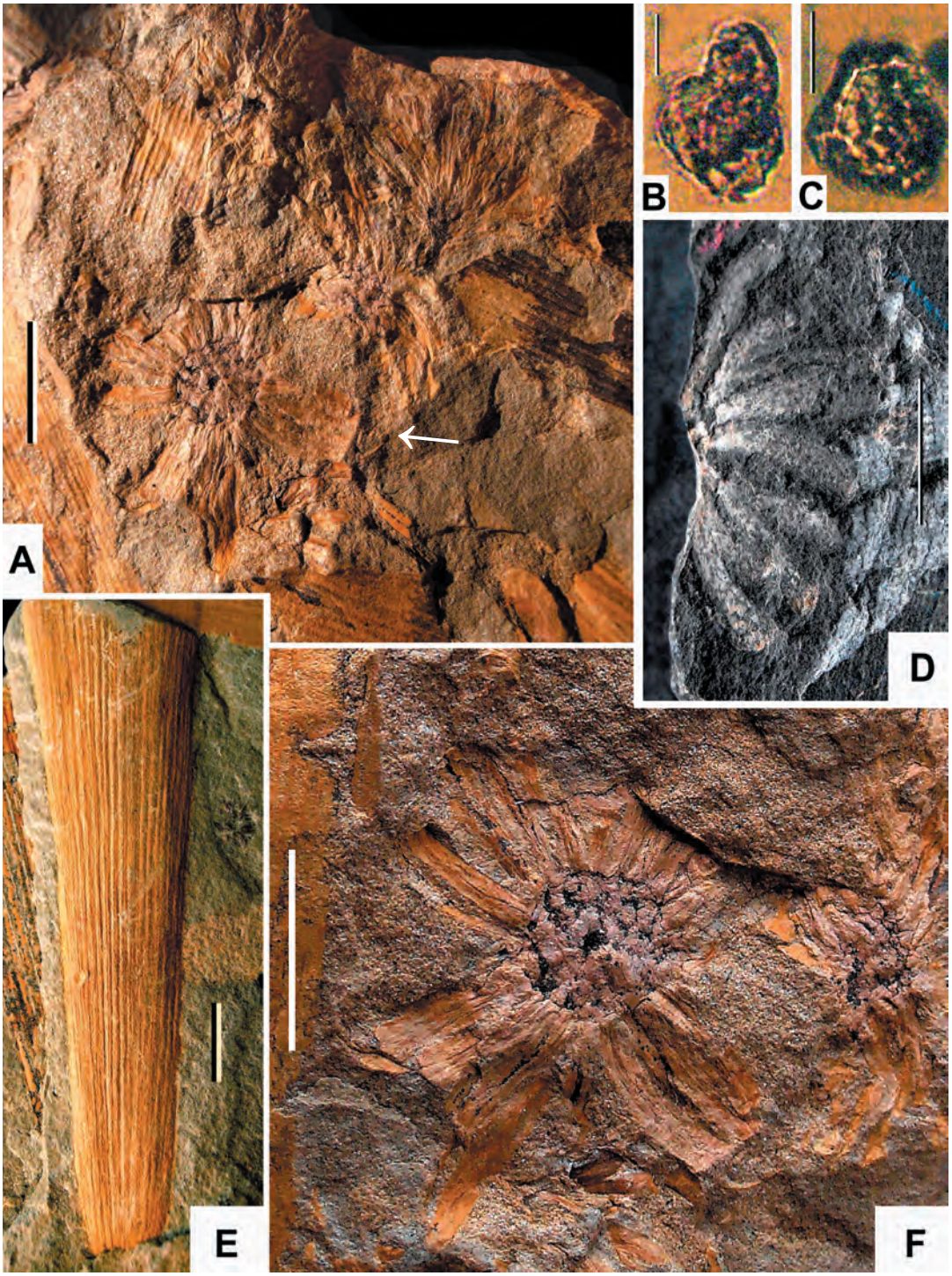


**Figure 1.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. (A–C, F), associated sterile leaf (E) and related form (D). A, F – holotype in front light, the rosette-like organ in the figure A, the holotype is marked by an arrow; B, C – pollen extracted from the microsporangia; B – pollen tetrad; C – individual anasulcate pollen grain; D – *Astrogaussia relaxata* (Radczenko) Naugolnykh; E – *Rufloria* sp. Localities: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk (A–C, E, F); Russian Far-East, Okhotsk region (D; for details see: Radczenko 1961). Scale bars = 1 cm (A, D–F); 15 µm (B, C).

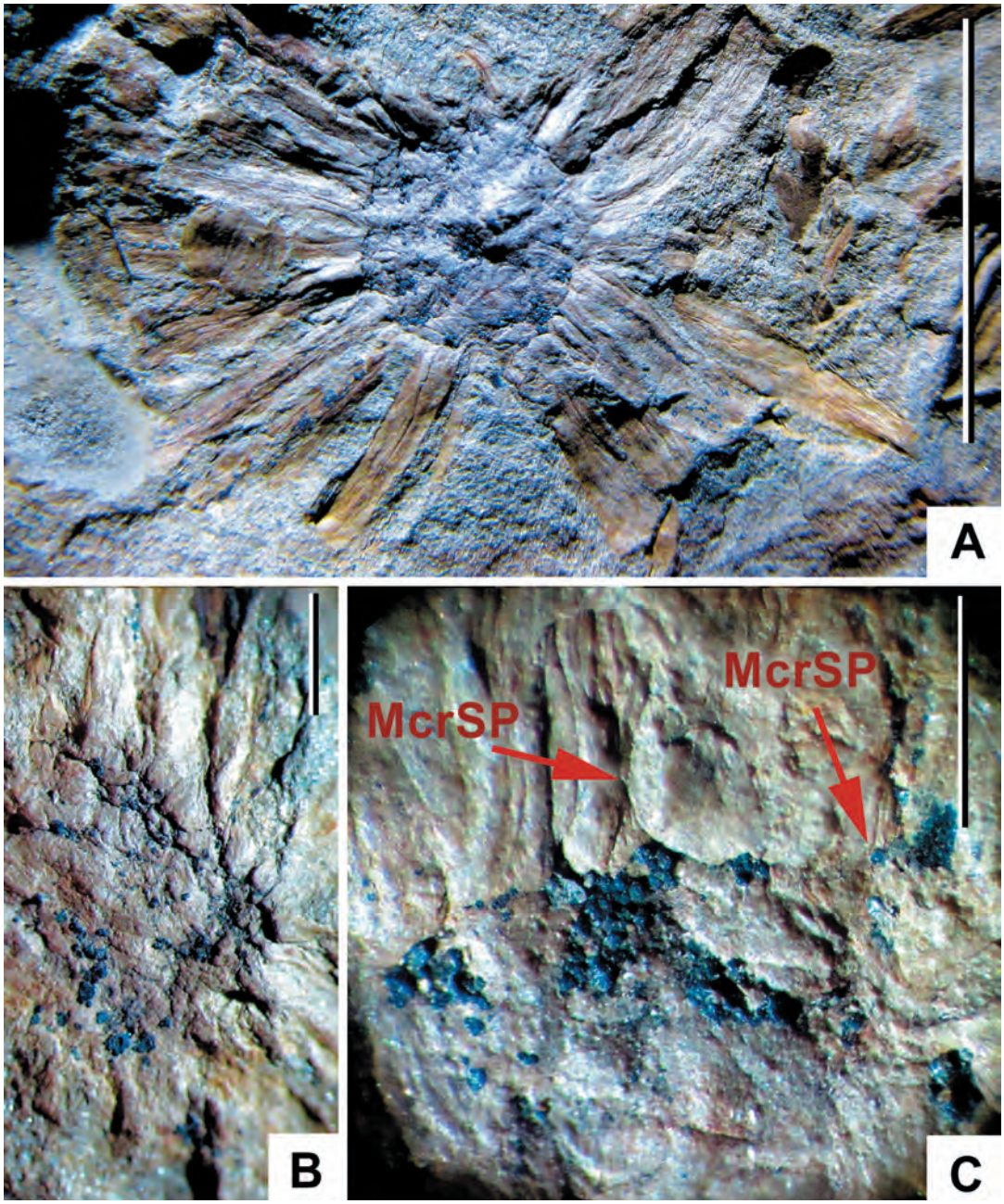


**Figure 2.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. A – the holotype in oblique light; B – transitional zone between microsporangia and radially arranged scales; C – microsporangia (McrSP) marked by red arrows. Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 cm (A); 1 mm (B, C).

Although the general architecture of these organs is similar to the genus *Astrogaussia* (see 'Comparison' chapter above and Fig. 1D), a presence of microsporangia does not allow to attribute this plant to the latter genus.

There are small (about 0.1 mm in diameter) round particles consisting of dense black coaly matter, disposed in peripheral zones of apical part of the axis, as a rule, between bases of the

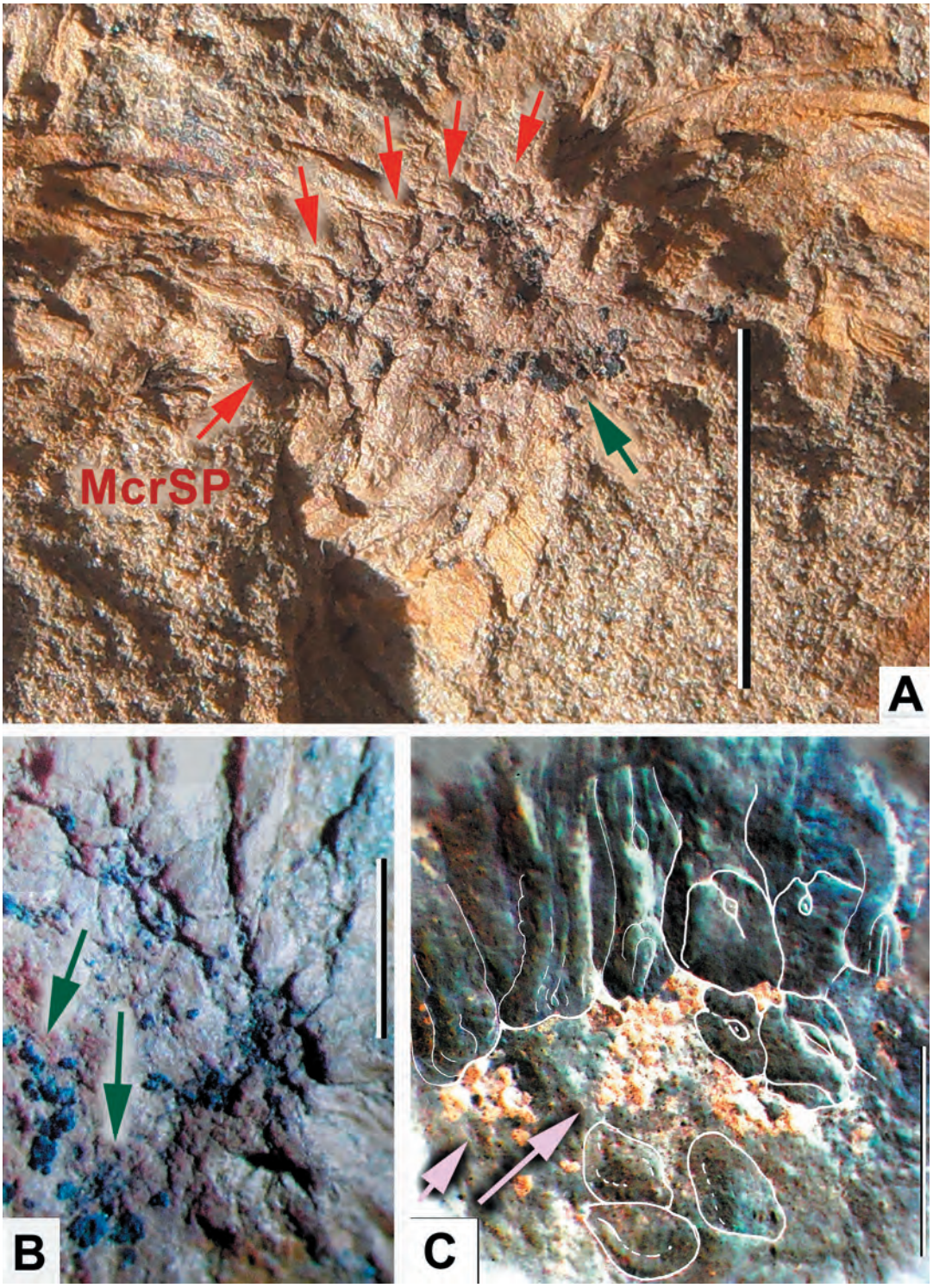


**Figure 3.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. A – the laterally deformed rosette-like organ; B – microsporangia; the glands are marked by the green arrows. C – inverted line tracing of microsporangia (here the glands are of bright orange color); the glands are marked by the rose arrows. Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 cm (A); 1 mm (B, C).

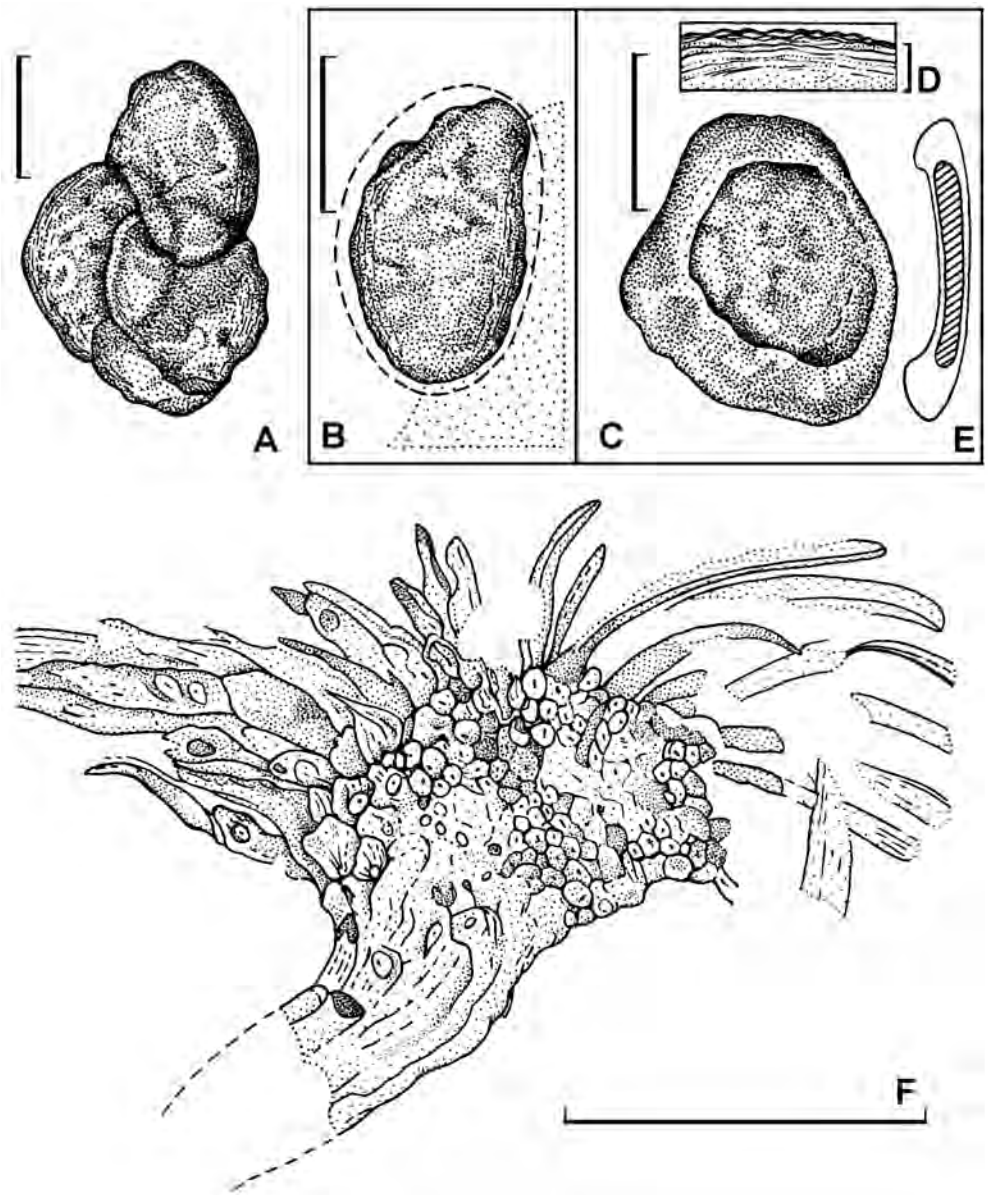


**Figure 4.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. A – tetrad of pollen (same tetrad is shown in Fig. 1B); B – diagenetically deformed individual pollen; C – anasulcate pollen grain; D – finely scabrate surface of pollen; E – the scheme of cross section of pollen (inner cavity is marked by oblique lines); F – laterally deformed rosette-like organ, numerous microsporangia are visible. Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 cm (F); 15 µm (A, B, C, E); 2 µm (D).

radial appendages and microsporangia (Fig. 3B, C). According to my point of view, these particles represent remnants of glands secreted/exudate special liquid chemicals for attracting insect pollinators.

There are eight isolated seeds preserved on the same bedding surface together with the reproductive organs under consideration. One well-preserved seed/ovule of the same morphological type was discovered after careful preparation being in natural connection to the proximal part of one of

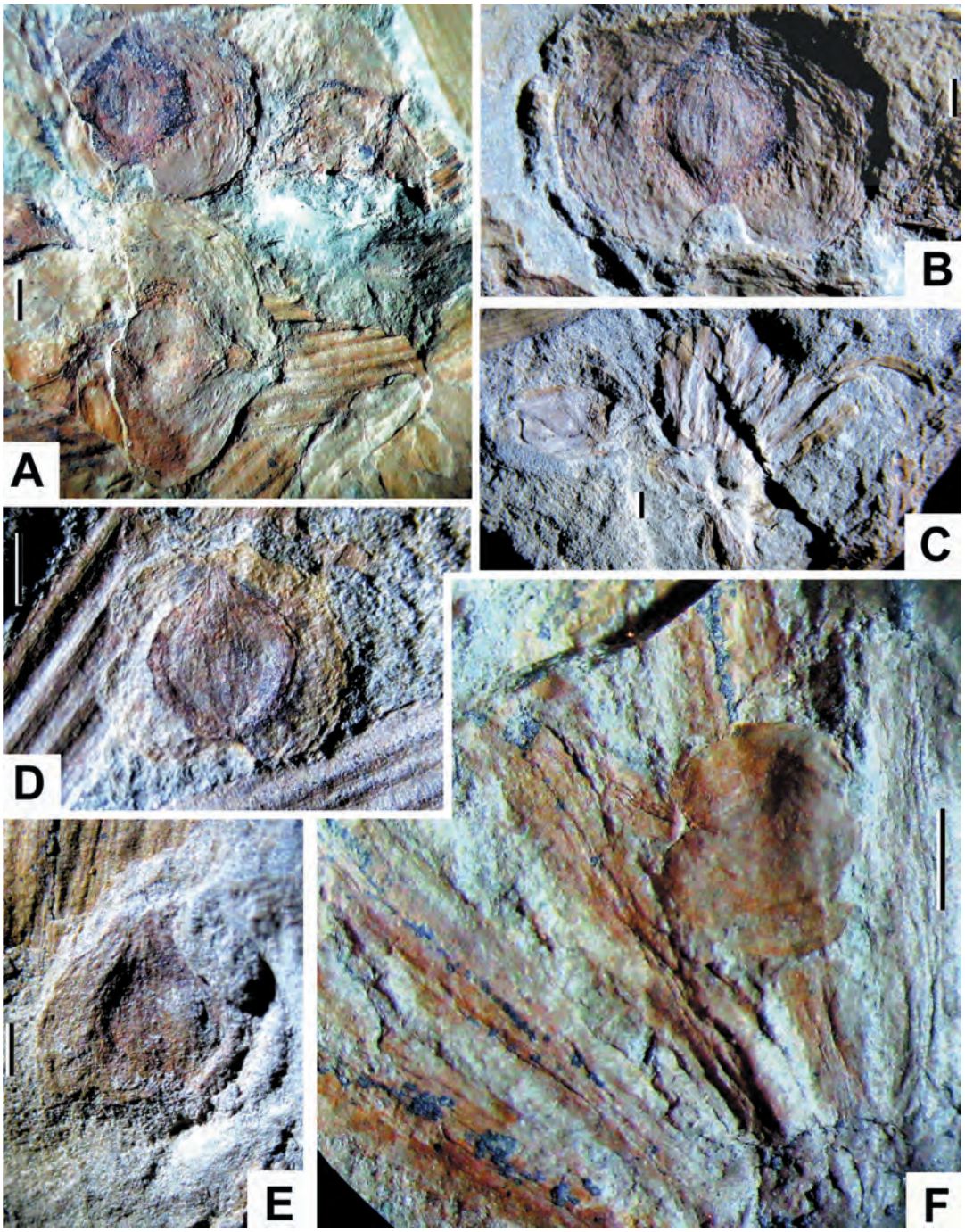


**Figure 5.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. The seeds found together with the reproductive organs (A–E) and in natural connection to the seed stalk (F). Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 mm (A–F).

the radial appendages (Figs 5F; 6A, B), and one more seed is found just nearby an appendage in a position, which is very close to natural (Figs 5C; 7B; 8B). As it was noted above, all of these seeds are of one and the same type. They are winged, with the wide limb surrounding the seed

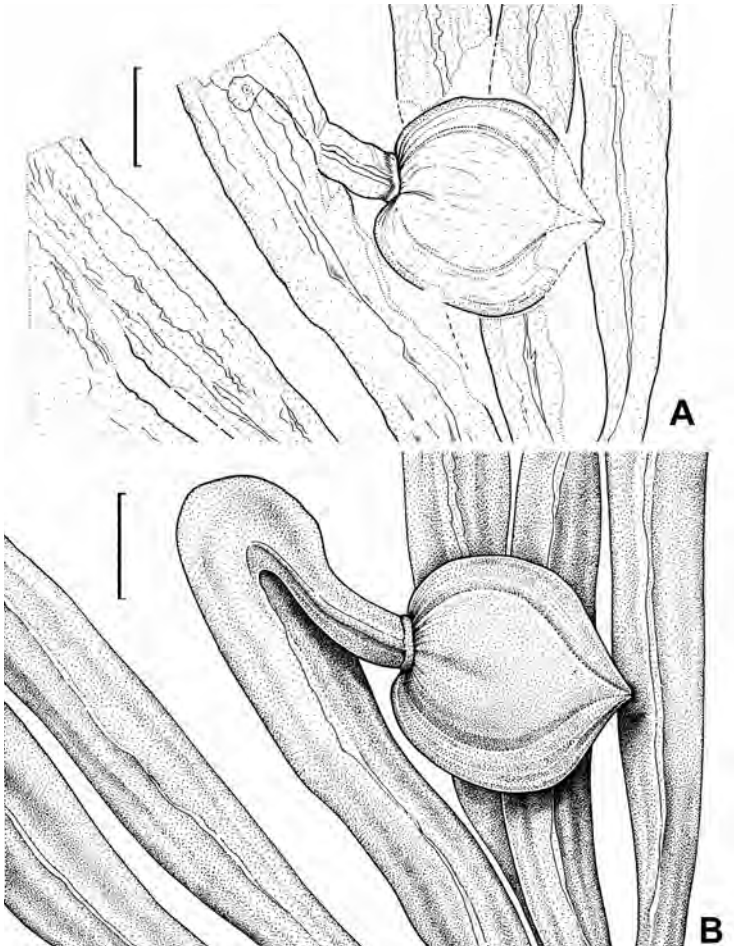


**Figure 6.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. The seed found in natural connection to the seed stalk. A – line drawing after photograph shown here on Fig. 5F; B – reconstruction of the seed attachment based on the line drawing. Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 mm (A–B).

base, with a small notch disposed just in the place, where the seed stalk was attached to the seed base. The wing is somewhat narrower around the micropylar part of the seed (Figs 5A–F; 6A, B; 7A–D, F, G; 8A–D, F, G). A central part of the seeds ('endosperm' or nucellus covered by a sarcotestal coat) bears distinct prolonged striation. Finer striation is observed on wings of some seeds as well (Figs 5A, B, D; 7C, F; 8C, D, F). Size of the seeds varies from 3 mm length and 4 mm width to 6 mm lenghts and 7 mm width; so width normally is slightly greater than length. General shape of the seeds is ovoid to cardioid, with an attenuate apex (micropylar part of the seed).

The seed preserved in natural connection to the radial appendage has the same structure, but is slightly smaller (2×2 mm). One can clearly see, how the conductive strand comes from the radial appendage into the seed base (Fig. 5F; 6A). Judging from the presence of the appendages with obtuse apex (there are at least three of such appendages per one reproductive organ), these can be interpreted as former seed stalks with detached seeds after their maturation.

The morphological characteristics of the reproductive organs given above is a basis for suggesting the reconstruction of *Archaeopetalanthus progressus* (Fig. 9).

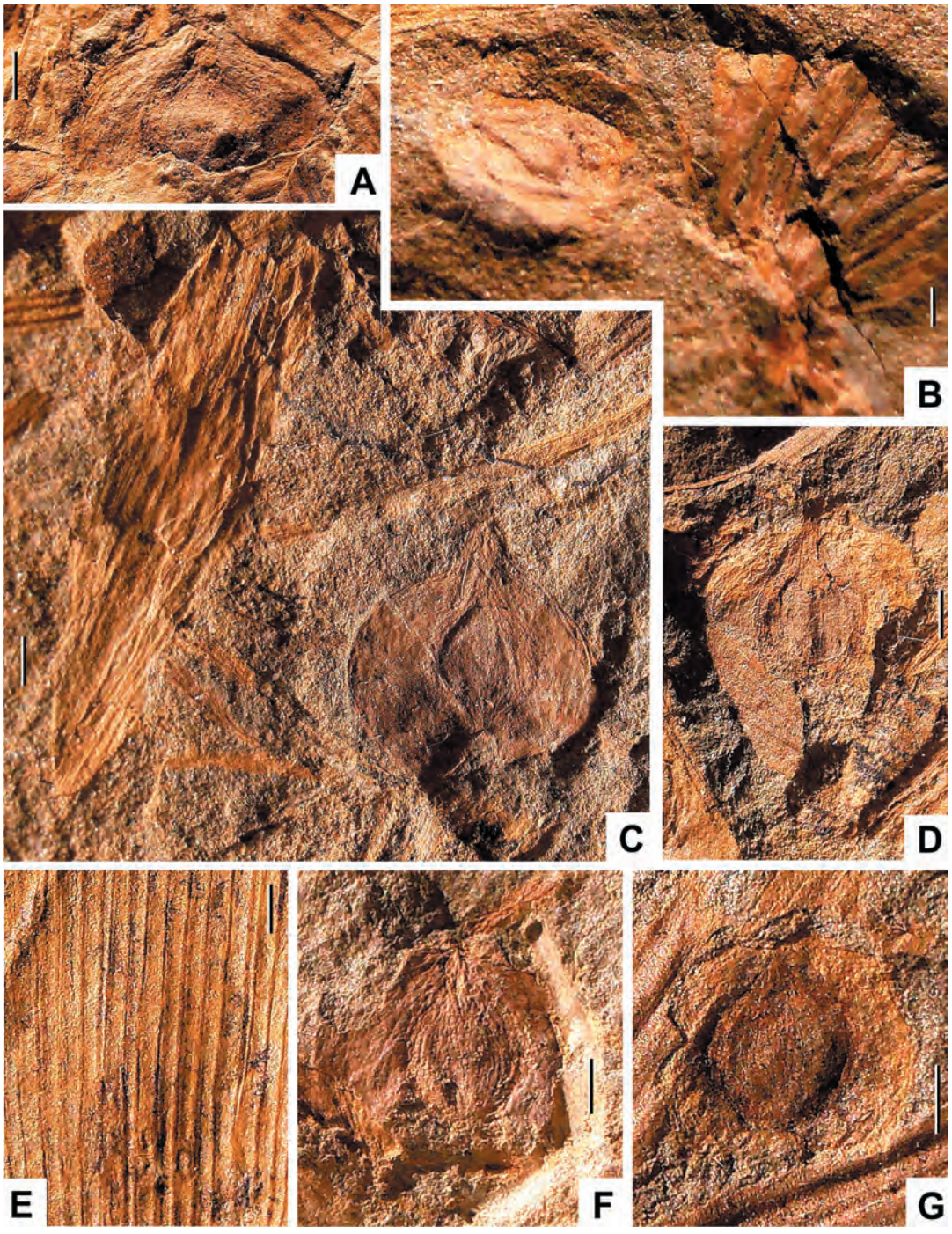


**Figure 7.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. The seeds and other organs found in close association with the reproductive organs (A–D, F, G); venation details of the *Rufloria* leaf from the same specimen (E). Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 mm (A–G).

The reproductive organs of *A. progressus* are reconstructed here as bisexual, with numerous microsporangia disposed on the upper surface of the apically widened obconic axis. Some of the microsporangia also could be placed on radially arranged appendages, which are disposed

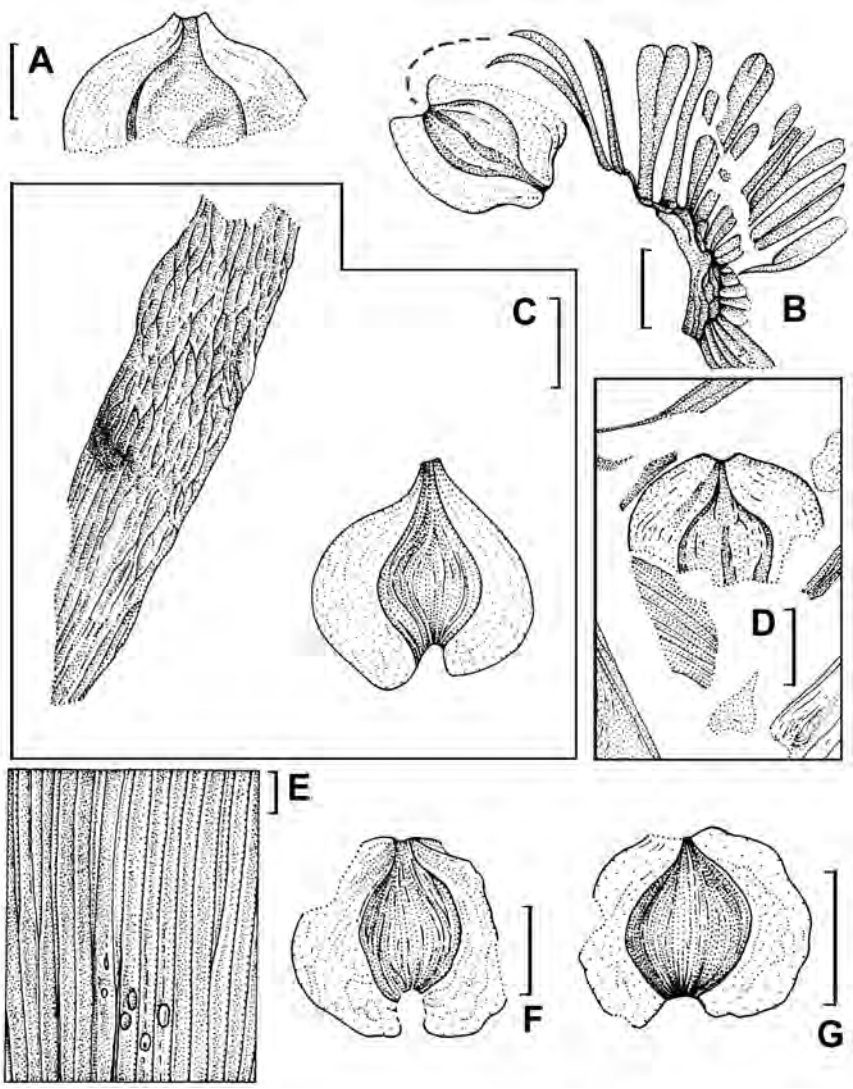


**Figure 8.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. The seeds and other organs found in close association with the reproductive organs (A–D, F, G); venation details of the *Rufloria* leaf from the same specimen (E). Line drawings after Fig. 7. Locality: Listvjanskaya Formation, Middle/Late Carboniferous; the right bank of the Kan River, mouth of the Mokhovoj Creek (Rivulet), upstream of the City of Kansk. Scale bars = 1 mm (E); 2 mm (A, C, D, F, G); 3 mm (B).

concentrically around the apical part of the axis. The appendages are long and narrow, petal-like. Some of them (at least, three per one reproductive organ) bear terminal seeds.

**Remarks.** There are numerous lanceolate leaves with parallel venation disposed on the same bedding surface together with the reproductive organs and also on other side of the specimen (Fig. 1E). All of these leaves are of one and the same morphological type and could be attributed to the genus *Rufloria* S. Meyen. The leaves of *Rufloria* are very typical elements of the Carboniferous and Permian floras of Angaraland. Similar, if not identical, leaves were reported from the Permian deposits of Gondwana (McLoughlin & Drinnan 1998). I am quite certain that the ruflorian leaves and the reproductive organs, which are described above in the present paper, belonged to one and the same parent plant.

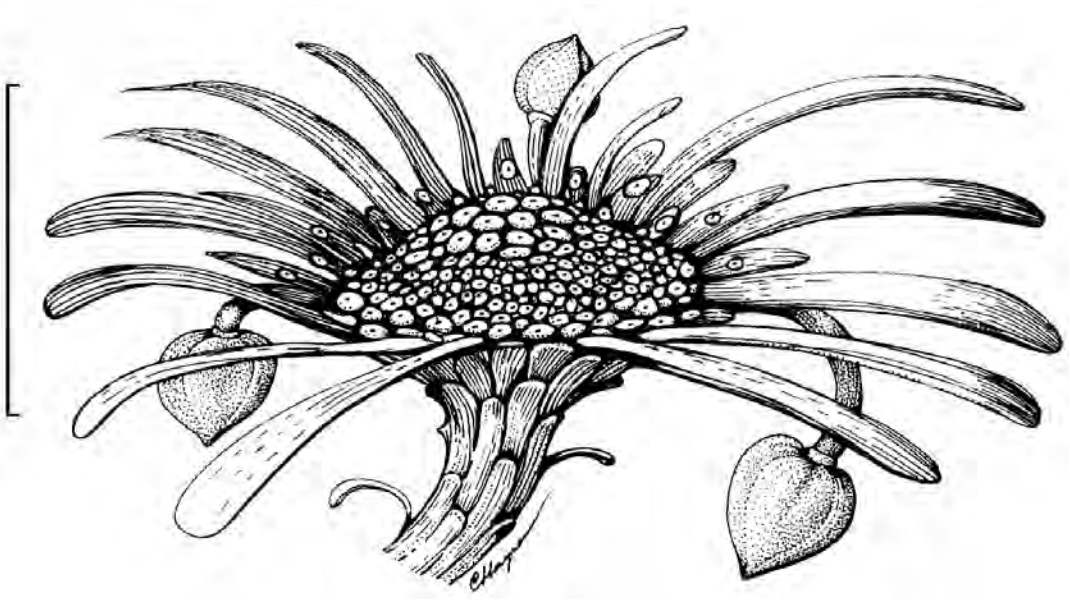

**Figure 9.** *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. Reconstruction of the bisexual reproductive rosette-like organ. Scale bar = 1 cm.

The *Rufloria* leaves found in close association with *Archaeopetalanthus progressus* have many features in common with the species *Rufloria theodorii* (Tschirkova et Zalessky) S. Meyen from the Alykaevsky floristic assemblage, with the exception of the presence of rare, thick, axial veins which are typical of *R. theodorii* (Betekhtina et al. 1988: Plate XXXII, fig. 1).

There are some similarities between seeds of *Archaeopetalanthus progressus* and the isolated seeds found in Alykaevsky floristic assemblage and described as *Samaropsis patula* Zalessky (Betekhtina et al. 1988: Plate XXXI, fig. 10; Sukhov 1969: Plate 4, fig. 7a).

## Discussion

The most impressive feature of *Archaeopetalanthus progressus* is its bisexuality and flower-like habit. According to *A. progressus* morphology, this plant cannot be interpreted as a direct predecessor of flowering plants or, being more precise, angiosperms, but nonetheless its characteristics clearly show that *A. progressus* was an evolutionary advanced gymnosperm and had no analogues in the Middle and Late Carboniferous vegetation around the world, at least as we know it up to the present time.

Anasulcate pollen of *A. progressus* lacking air sacs/balloons together with the bisexual nature of these reproductive organs point to a possible way of pollination of this plant. It is obvious that the critical point of exchange of genetic material for such bisexual organs is cross-pollination. In Late Palaeozoic, and especially in Carboniferous, only arthropods, mostly insects, could be agents for such cross-pollination. The small glands disposed nearby the microsporangia of *A. progressus* could exudate aromatic chemicals for attracting insects/pollinators (for example, *Goldenbergia* Scudder, Fig. 10), which had trunk-like jaws for sucking juice from microsporangia, rich in hydrocarbons and amino-acids. Similar ethological reproductive patterns were suggested for some other Permian gymnosperms (Naugolnykh 2018, 2019).

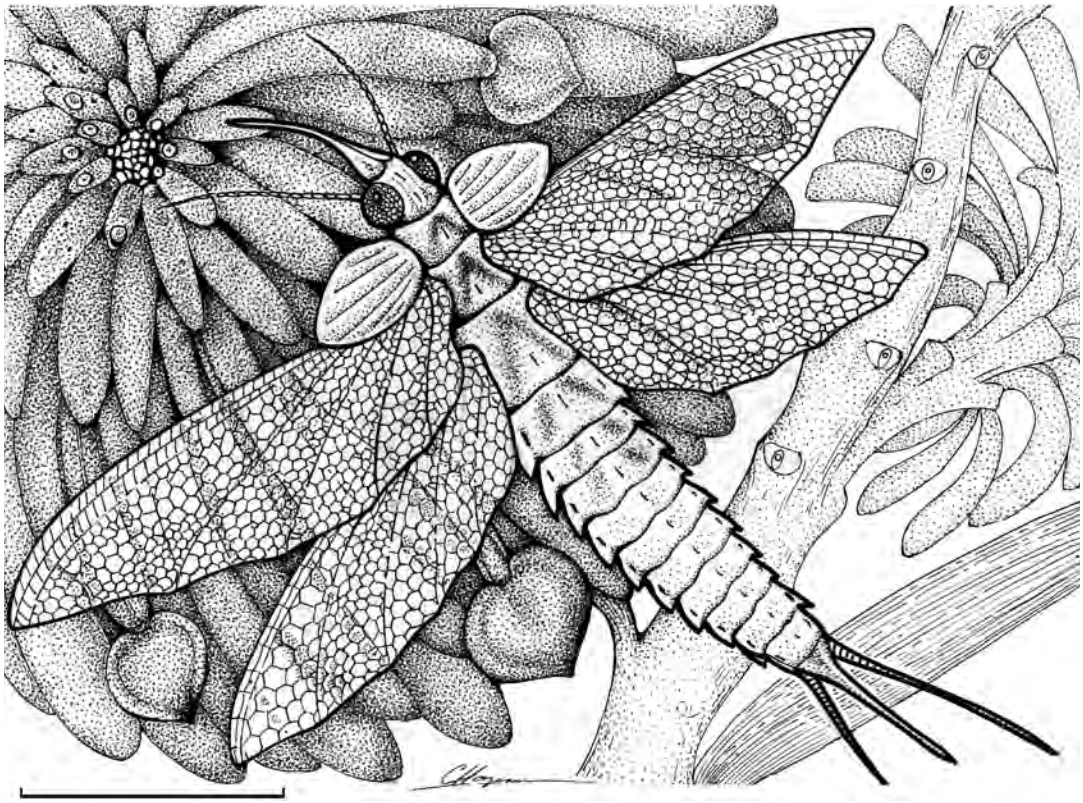

**Figure 10.** The insect *Goldenbergia* Scudder is feeding on the reproductive organ *Archaeopetalanthus progressus* Naugolnykh, gen. et sp. nov. Nervation of the insect wings is shown schematically. Scale bar = 1 cm.

## Acknowledgements

This work was funded by the State Program No 0135-2019-0044 of the Geological Institute of Russian Academy of Sciences 'Phytostratigraphy, palaeofloristics, crises events in Cenozoic, Mesozoic, and Palaeozoic of the various regions of Eurasia; palaeoclimatic, palaeophytocoenotic and palaeophytogeographical reconstructions', and RFBR project No 18-04-00322.

The author expresses his sincere gratitude to V.E. Sivchikov (the City of Novokuznetsk, Russia), who provided the specimen for this study. Colleagues N.M. Kadlets and T.V. Vinogradova from the Tchernyshev Central Scientific-Research Geological Museum (TsNIGR Museum, St. Petersburg) are gratefully acknowledged for their kind and helpful assistance in working with the *Astrogaussia* (al. *Gaussia*) *relaxata* (Radczenko) Naugolnykh specimen, which is kept in TsNIGR Museum, St. Petersburg, Russia.

## References

**Betekhtina O.A., Gorelova S.G., Drjagina L.L., Danilov V.I., Batyaeva S.P. & Tokareva P.A. (1988):** Upper Palaeozoic of Angaraland. Fauna and flora. – Novosibirsk: Nauka, Siberian office.

**Doweld A.B. (2004):** *Paravojnovskya*, a new substitute name for *Gaussia* (Vojnovskyales) based on fossil female fructifications. – Taxon **53**(2): 553–554.

**Doweld A.B. & Naugolnykh S.V. (2002):** *Scirostrobus* – a new replacement name for *Pholidophyllum* Zalessky, 1937 (Vojnovskyales, Pinophyta). – Paleontol. J. **36**(3): 322.

**Ignatiev I.A. (1988):** *Pukhontella* – a new genus of Rufloriaceae from the Permian of Angaraland. – Paleontol. J. **1**: 83–91.

**Ignatiev I.A. (2001):** On the morphology of cordaitean fructifications of *Krylovia sibirica* Chachlov from the Carboniferous of Siberia. – Paleontol. J. **2**: 103–108.

**Ignatiev I.A. (2011):** Morphology and systematic position of *Pholidophyllum ornatum* Zalessky strobili from the Kungurian of the Middle Fore-Urals. – Lethaea Rossica **4**: 40–49.

**Ignatiev I.A. & Meyen S.V. (1989):** *Suchoviella* gen. nov. from the Permian of Angaraland and a review of systematics of Cordaitanthales. – Rev. Palaeobot. Palynol. **57**: 313–339.

**Krassilov V.A. & Burago V.I. (1981):** New interpretation of *Gaussia* (Vojnovskyales). – Rev. Palaeobot. Palynol. **32**: 227–237.

**McLoughlin S. & Drinnan A.N. (1996):** Anatomically preserved Permian *Noeggerathiopsis* leaves from east Antarctica. – Rev. Palaeobot. Palynol. **92**: 207–227.

**Meyen S.V. (1982):** The Carboniferous and Permian floras of Angaraland: a synthesis. – Biol. Mem. **7**: 1–109.

**Meyen S.V. (1984):** Basic features of gymnosperm systematics and phylogeny as shown by the fossil record. – Bot. Rev. **50**(1): 1–111.

**Meyen S.V. (1987):** Fundamentals of palaeobotany. – London: Chapman and Hall.

**Meyen S.V. (1988):** Gymnosperms of the Angara flora. – In: Beck C.B. [ed.]: Origin and evolution of Gymnosperms: 338–381. – New York: Columbia University Press.

**Meyen S.V. (1990):** Theoretical problems of palaeobotany. – Moscow: Nauka.

**Naugolnykh S.V. (2001):** Morphology and systematics of representatives of Vojnovskyales. – Paleontol. J. **35**(5): 545–556.

**Naugolnykh S.V. (2010):** Gymnosperms of the classis Vojnovskyopsida; a new view on old problems. – In: Palaeontology and stratigraphy of the Permian system in museum expositions and private collections. Collection of scientific articles: 10–18. – Kungur, Perm: Polygraph City.

**Naugolnykh S.V. (2014):** Fossil flora and stratigraphy of the terrigenous Kungurian beds (Lower Permian) of the basin of the Barda River (Urals, Perm krai). – Strat. Geol. Correlation **22**(7): 680–707.

**Naugolnykh S.V. (2018):** A new concept and a newly emended diagnosis of the advanced peltasperm *Kuvakospermum pedatum* Naug. et Sidorov, emend. nov. from the Kazanian (Middle Permian) deposits of Russia. – Wulfenia **25**: 1–14.

**Naugolnykh S.V. (2019):** *Quasistrobus* Vladimirovich, 1986, emend. nov., a new interpretation of an advanced angaropeltian gymnosperm from the Middle Permian (Wordian) deposits of the Volga river basin, Russia – Wulfenia **26**: 37–52.

**Neuburg M.F. (1934):** Studies of stratigraphy of the coal-bearing deposits of the Kuznetsk Basin in 1930–1931. – Trudy Vses. Geol.-razved. Ob-ed. NKTP SSSR **348**: 3–47.

**Neuburg M.F. (1948):** Upper Palaeozoic flora of the Kuztesk Basin. – Moscow, Leningrad: Academy of Sciences of the USSR. [In Russian]

**Neuburg M.F. (1965):** Permian flora of the Pechora Basin. Part III. Cordaitales, Vojnovskyales, seeds of gymnosperms of uncertain systematic position (Semina gymnospermarum incertae sedis). – Moscow: Nauka. (Transactions of Geological Institute of Russian Academy of Sciences, Iss. 116). [In Russian]

**Radczenko G.P. (1933):** Fossil flora of Kolchuginskaya Formation of coal-bearing deposits of the Kuznetsk Basin. – Ann. Geol. Inst. Acad. Sci. **3**: 219–250. [In Russian]

**Radczenko G.P. (1961):** Early Permian flora in the Okhotsk town area. – Mat. Geol. Polezn. Iskop. Severo-Vostoka SSSR **15**: 214–226.

**Rothwell G.W., Mapes G. & Mapes R.H. (1996):** Anatomically preserved vojnovskyalean seed plants in Upper Pennsylvanian (Stephanian) marine shales of North America. – J. Paleontol. **70**(6): 1067–1079.

**Savitskaja L.A. (1970):** About Carboniferous flora of the Gissar and Kuramin ridges. – In: Biostratigraphy of the sedimentary formations of Uzbekistan: 110–129. – Leningrad: Nedra. [In Russian]

**Sixtel T.A., Savitskaya L.I. & Iskandarkhodzhaev T.A. (1975):** Plants of the Middle Carboniferous, Upper Carboniferous and Lower Permian of Fergana. – In: Sixtel T.A. [ed.]: Biostratigraphy of the Upper Palaeozoic of the mounting frames of Southern Fergana: 77–143. – Tashkent: FAN. [In Russian]

**Sukhov S.V. (1969):** Seeds of the Late Palaeozoic plants of the Middle Siberia. – Leningrad: Nedra.

**Wendland H.A. (1865):** Über die neue Palmengattung *Gaussia*. – Nachr. Königl. Ges. Wiss. Georg-Augusts-Univ. 1865: 327–329.

**Zalessky M.D. (1934):** Observations sur les végétaux nouveaux du terrain permien du Bassin de Kousnetsk, II. – Bull. Acad. Sci. URSS **5**: 743–775.

**Zalessky M.D. (1937):** Contribution à la flore permienne du basin de Kousnetzk (accompagnée d'une note sur deux plantes jurassiques du même bassin). – Probl. Paleontol. **2/3**: 125–142.

**Zimina V.G. (1967):** A first find of *Vojnovskya* in the Permian deposits of the Southern Primorie. – Paleontol. J. **4**: 112–117.

Address of the author:

Serge V. Naugolnykh
Geological Institute, Russian Academy of Sciences
Pyzhevsky per. 7
119017 Moscow, Russia
E-mail: naugolnykh@rambler.ru
naugolnykh@list.ru