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A new Carboniferous pteridosperm of Angaraland: *Angaranthus victorii* Naugolnykh, gen. et spec. nov. (Angaranthaceae, fam. nov., Callistophytales)

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Summary: Angaranthus victorii Naugolnykh, a new genus and species is described based on material from the Middle Carboniferous of Angaraland (Siberia). The new genus possesses modified fertile fronds bearing fusiform microsporangia which form lax clusters on lateral extensions (modified pinnae) of the fertile frond. These new male organs are associated with *Angaridium*-type monopinnate sterile fronds with pinnules dissected to a different extent. Angaranthaceae, a new family is established for Angaran Callistophytalean pteridosperms of the genera *Angaranthus, Angaridium, Angarocarpus, Gondwanotheca, Paragondwanidium.*

Keywords: gymnosperms, pteridosperms, Carboniferous, Angaraland, fam. nov., gen. nov., spec. nov., Angaranthaceae, *Angaranthus*, *Angaridium*, *Angarocarpus*, *Paragondwanidium*, *Gondwanotheca*

There are many different leaf-based genera among Carboniferous pteridosperms and pteridophytes, whose exact taxonomical position is still enigmatic, mostly because we have no data about their reproductive organs. One of these plants is *Angaridium* Zalessky, established on the basis of sterile fronds only. Meyen (1988) believed that this plant had *Angarocarpus*-type seeds, although they had never been found in natural connection to each other. The same seeds were attributed to the genus *Paragondwanidium* Meyen (Meyen 1988) also on the basis of the accompanying association. Leaves of *Paragondwanidium* and *Angaridium* resemble each other and certainly originated from the common ancestor somewhere in the Early Carboniferous.

Later on, one fertile organ assigned to *Gondwanotheca* (?) sp. was described and figured by Sivchikov (1996). This specimen came from Chernogorskaya Formation (Abakan River Basin, Siberia). This stratigraphic level in Angaraland (Mazurovskaya Formation and its stratigraphically equivalent strata) is characterized by abundant leaves of the genus *Angaridium*, commonly attributed to different species: *A. tenuis* Gorelova, *A. potaninii* (Schmalhausen) Zalessky, *A. submongolicum* Neuburg, *A. mongolicum* Zalessky, *A. finale* Neuburg (Betekhtina et al. 1988). The general habit of the female reproductive organs of *Gondwanotheca* Neuburg described and figured by Neuburg (1948: Plate XXXVIII, Figs 5–8; later redrawn by S. V. Meyen and ascribed to *Paragondwanidium* Meyen (Meyen 1982, 1987, 1988)), and its seed-bearing organs illustrated by Sivchikov (1996: 58, Fig. 3) is similar to basal parts of some *Angaridium* leaves (see Discussion below). According to the author's viewpoint, these female fructifications could belong to pteridosperms with *Angaridium* leaves and *Angaranthus* male reproductive organs (see Description below). No evidence of male fructifications either for *Paragondwanidium* or for *Angaridium* has been published so far. The present paper deals with the first report on male reproductive organs taphonomically linked with the foliage of *Angaridium.*

Materials and methods

The material examined was provided by Mr. V. E. Sivchikov (Novokuznetsk, Russia). It originated from the Listvjazhninskaya Formation (stratigraphic equivalent of the Katskaya and Mazurovskaya Formations, upper part of the Mazurovskian Horizon; for comments see: Rasskasova 1962). The locality (Fig. 1) is on the right bank of Kan River, near the eastern part of Kansk, close to the mouth of Mohovoi Rivulet. The collection studied includes specimens mostly preserved as impressions, but sometimes with poorly preserved compressed plant tissues. The impressions are preserved in dense light-grey clayey shales of limnic origin. The plant megafossils form monodominant taphocoenosis with predominant leaves of *Angaridium* of several types, which are linked by intermediate forms (see Discussion below) with parts of fertile fronds probably all belonging to one and the same parent plant. The collection is kept at the Geological Institute of Russian Academy of Sciences (GIN RAS) Moscow under number 4846 (the author's Angaran collection).

Several specimens of sterile and fertile organs of pteridosperms of Angaranthaceae kept at the Central Scientific-Research Geological Museum named after Tchernyshev (TsNIGR Museum, St Petersburg) are also figured (Fig. 8 A, C–F) and discussed in the present paper. Age and geographical position of these specimens are given in the figure caption.

Current terminology for the description of compound pinnate leaves is used for characteristics of sterile leaves. The same terms were applied to the male fertile fronds from one and the same locality, except the terms for last order units, which are called here 'last order fertile segments' but not pinnules.

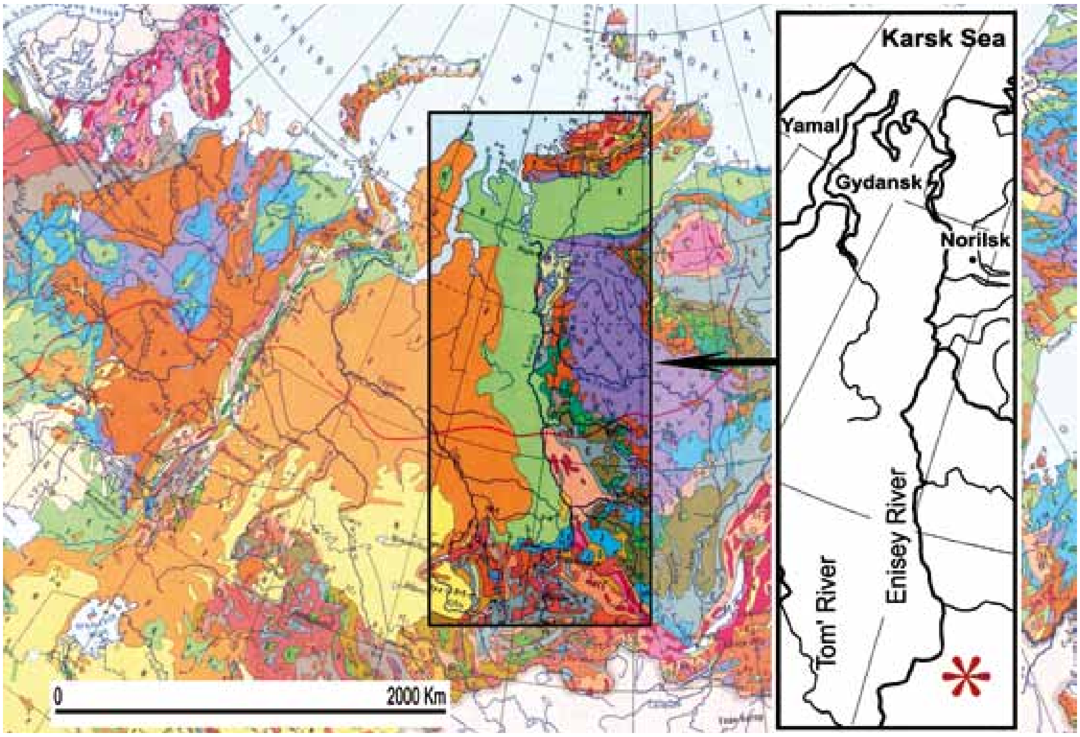

Figure 1. Geographical position of the locality of *Angaranthus victorii* Naug., sp. nov. (marked by the red asterisk). Source of geological map: http://www.jurassic.ru

Systematics and description

Pteridospermae (Lyginopteridophyta)

Classis Lyginopteridopsida Novak, 1961

Ordo Callistophytales Rothwell, 1981

Family **Angaranthaceae Naugolnykh, fam. nov.**

Type genus. *Angaranthus* Naugolnykh, gen. nov.

Diagnosis. Pteridosperms with compound monopinnate leaves consist of rachis and subtriangular fan-shaped pinnules. Pinnules from entire-margined to deeply dissected with linear lobes. Female reproductive organs are fertile fronds with reduced pinnae bearing winged ovules of *Angarocarpus*-type. Male reproductive organs are fertile fronds with reduced leaf lamina, with lateral extensions homologous to normal sterile pinnae bearing last order fertile segments. These fertile segments bear lax clusters of microsporangiate polliniferous organs consisting of microsporangia. Microsporangia are fusiform, attached by their base to the fertile segments.

Composition. Type genus *Angaranthus* and the genera *Angaridium, Angarocarpus, Gondwanotheca, Paragondwanidium.* Probably most of the Angaran species of the former genus *Rhodea* (currently *Rhodeopteridium*; see here Fig. 8 F) should also be attributed to this family.

Distribution. Middle Carboniferous, Siberia, Russia; northern Kazakhstan.

Angaranthus **Naugolnykh, gen. nov.**

Type species. *Angaranthus victorii* Naugolnykh, sp. nov., Middle Carboniferous, Listvjazhninskaya Formation, Siberia, Russia.

Diagnosis. Male reproductive organs form monopinnate fertile fronds without leaf lamina, with lateral extensions bearing last order fertile segments. These fertile segments have clusters of microsporangiate polliniferous organs consisting of microsporangia. Microsporangia are fusiform with acute apices forming lax radial aggregations of three to five sporangia. Prepollen preserved *in situ* are of *Plicatipollenites*-type.

Comparison. The new genus differs from the closely related genera *Permotheca* Zalessky, *Pterispermastrobus* Remy and *Callipterianthus* Roselt in a non-synangiate (not fused) aggregation of microsporangia.

Distribution. Middle Carboniferous, Listvjazhninskaya Formation, Siberia, Russia.

Angaranthus victorii **Naugolnykh, sp. nov.** (Figs 2–7, 9 B, 10)

Derivatio nomini. Named after the geologist Victor E. Sivchikov who collected the fossil remains of *Angaranthus victorii.*

Holotype. Fig. 2 D–F; Fig. 3, Fig. 10 A–E; GIN 4846/146a, counterpart of the holotype – 4846/148a; Kansk locality, the right bank of Kan River, near the eastern part of Kansk close to the mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation Siberia, Russia. Syntypes: 4846/149, 4846/150. Types are kept at the Geological Institute of Russian Academy of Sciences (GIN RAS) Moscow.

Figure 2. Morphology of male fructifications of *Angaranthus victorii* Naug., sp. nov. and associated sterile leaves of *Angaridium* sp. A–B – syntype 4846/149a; C, E – syntype 4846/150a; D – holotype 4846/148a; F – holotype 4846/146a. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars = 1 cm.

Description. The material studied includes the basal and the apical parts of the well-developed fertile fronds. Three almost completely preserved sterile fronds and several fragments as well as some isolated pinnules were also attributed to the same species.

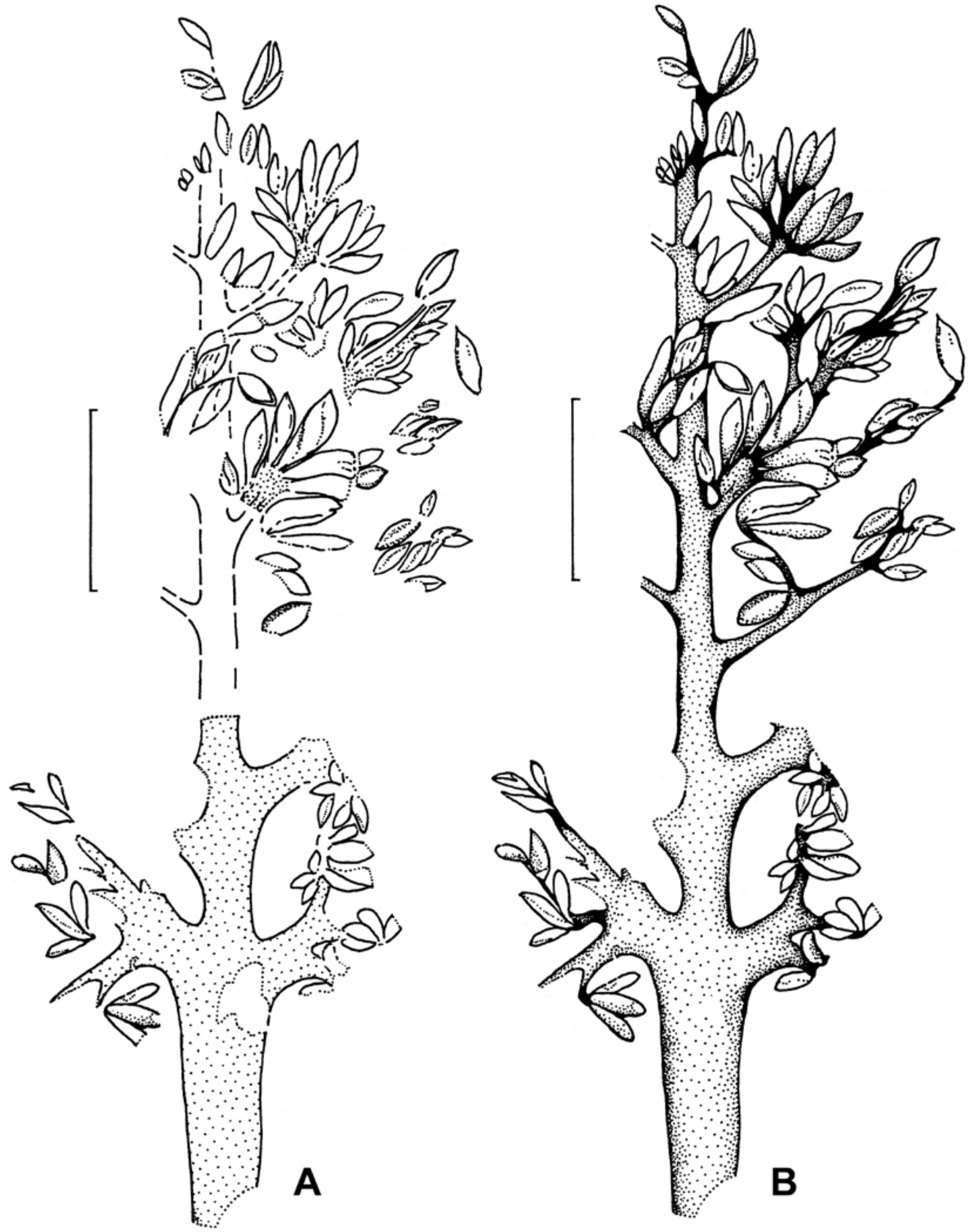

Figure 3. Morphology of male fructifications of *Angaranthus victorii* Naug., sp. nov. A – combined line tracing of the apical part of the fructification based on the syntype 4846/149a, and the basal part of the fructification based on holotype 4846/146a. B – reconstruction of the male fructification. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars = 1 cm.

Sterile fronds are monopinnate, approximately 8 cm long and 4 cm wide, with imparipinnate apex and flattened rachis bearing fine longitudinal striation. Last order segments (pinnules) are subtriangular, cuneate at base and with a wide apex, and are attached to the frond rachis at an

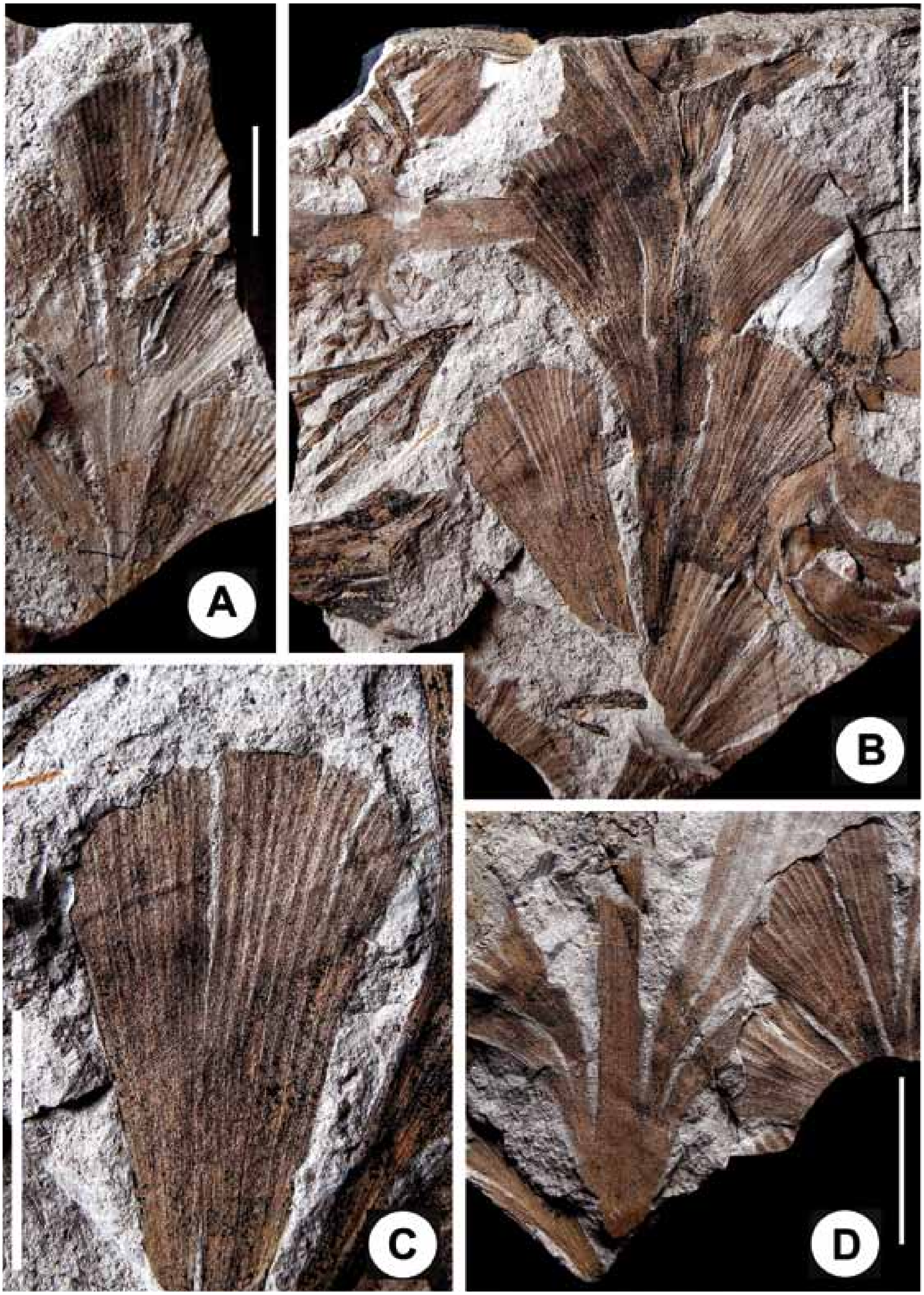

Figure 4. Morphology of male fructifications of *Angaranthus victorii* Naug., sp. nov. and associated sterile leaves of *Angaridium* sp. A – apical part of the sterile frond, spec. 4846/146d; B – middle part of the sterile frond, spec. 4846/146b; C – bilobate pinnule with cuneate base, spec. 4846/146b; D – middle part of the frond in association with the frond apex, spec. 4846/150d–e. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars = 1 cm.

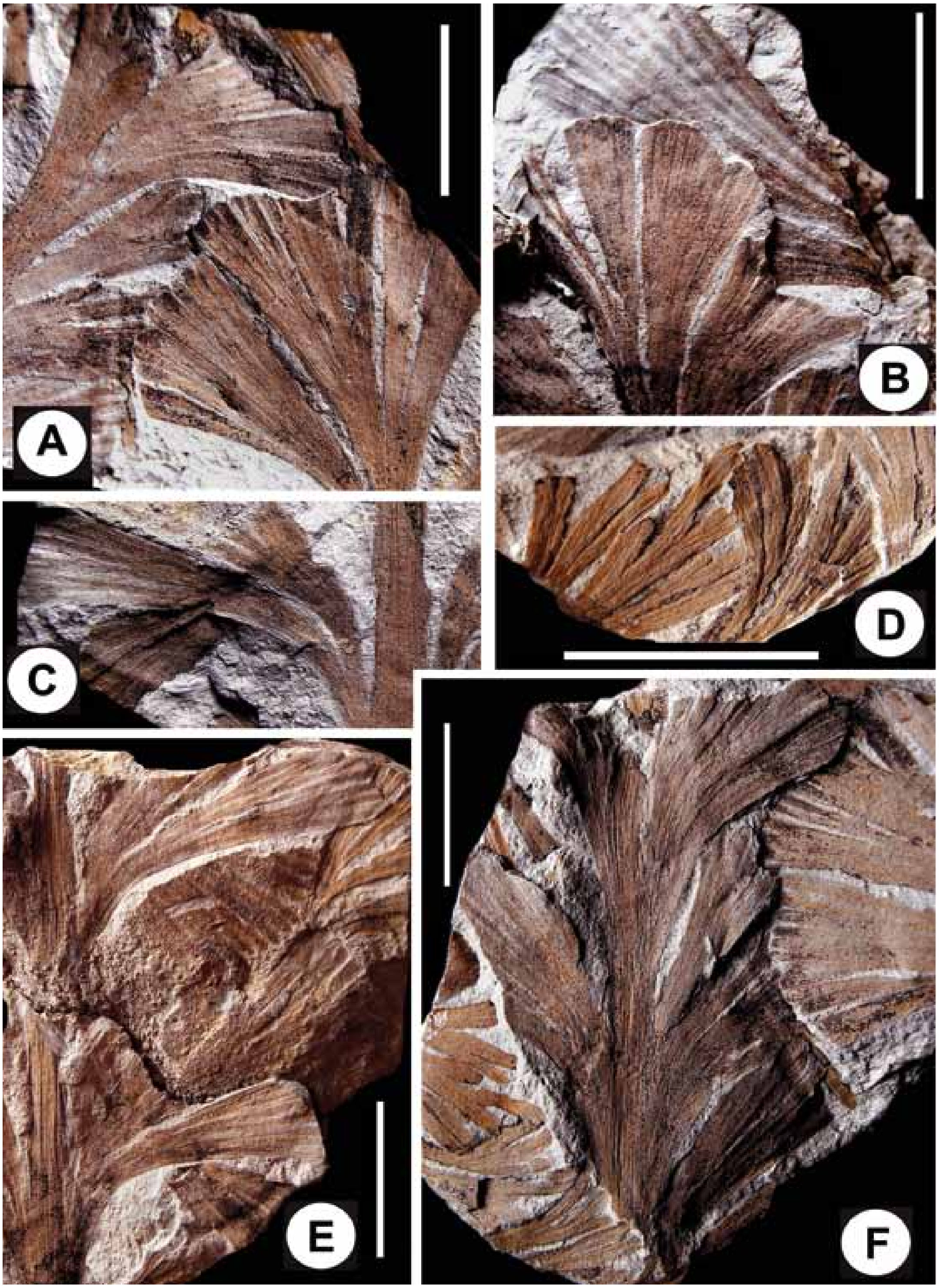

Figure 5. Morphology of sterile leaves of *Angaridium* sp., associated with the male fructifications of *Angaranthus victorii* Naug., sp. nov. A – middle part of the frond, left (spec. 4846/151b), and apical part of the frond, spec. 4846/151a; B – apical part of the frond, spec. 4846/147a; C – middle part of the frond having well-developed pinnules with cuneate bases, 4846/150d; D – deeply dissected pinnules, spec. 4846/151; E – middle part of the frond, spec. 4846/152; F – middle part of the frond, spec. 4846/151b. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars = 1 cm.

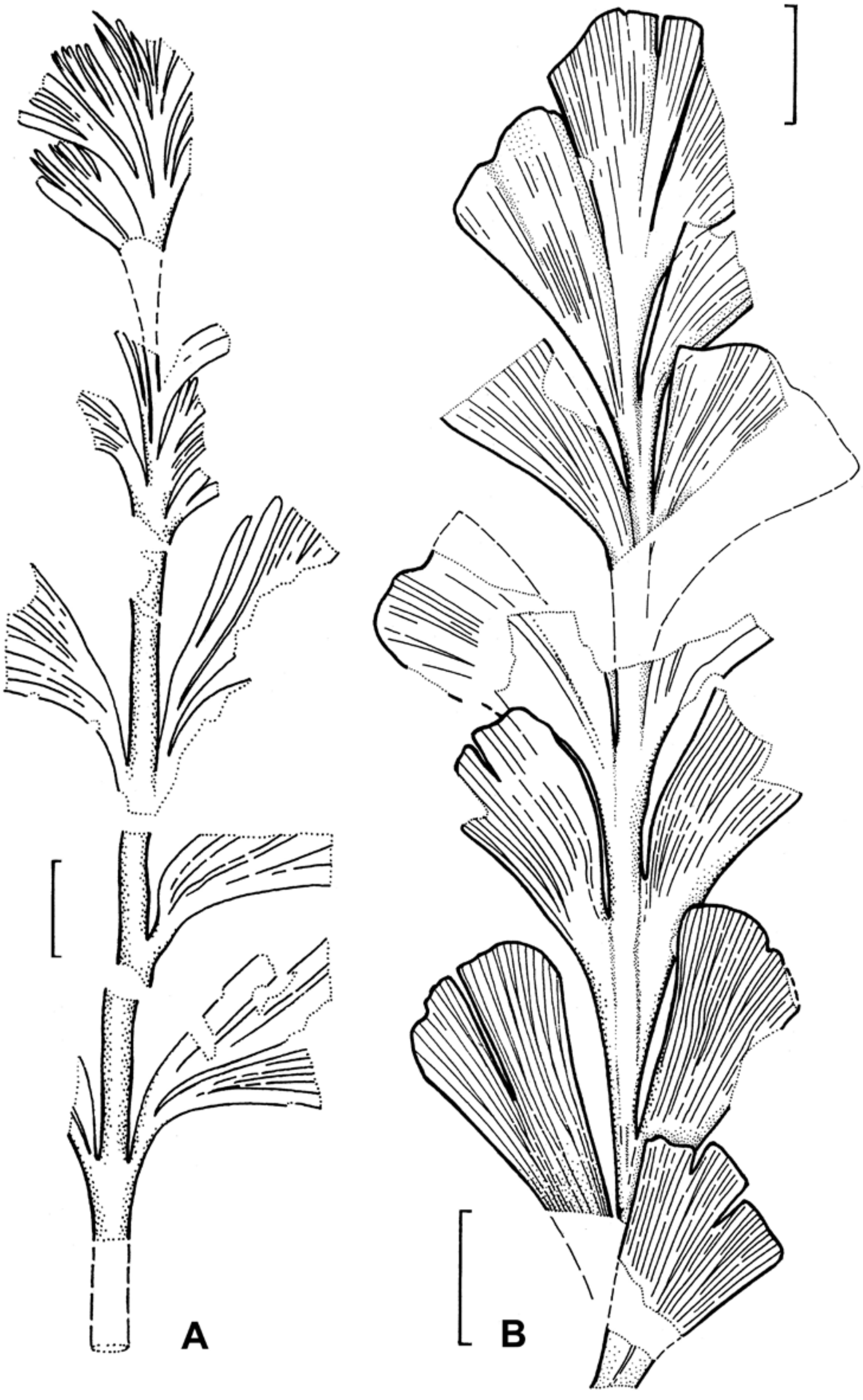

Figure 6. Morphology of sterile leaves of *Angaridium* sp., associated with the male fructifications of *Angaranthus victorii* Naug., sp. nov. Line tracings. A – frond modification with the deeply dissected pinnules, based upon the specimens (top down): 4846/149d, 4846/151b, 4846/150d, 4846/152; B – frond modification with the almost entire-margined pinnules, after specimens 4846/146d, 4846/146a. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars = 1 cm.

angle of 30–40°. Average pinnule length is 2 cm, width is 1 cm. Pinnules are entire-margined to deeply dissected to linear or lanceolate lobes. Venation is fan-shaped, without any midvein. Veins are thin, simple or once to twice dichotomizing.

Fertile fronds are monopinnate, total length is unknown, but judging by size of the basal part, it could reach 10 cm in length and 5 cm in width. Basal part of the fertile frond is cuneate. Rachis is relatively thick, up to 6 mm wide. It bears lateral extensions which could be dichotomized one or two times. The extensions are attached to the fertile frond at an angle of 40–45°. The most well-developed lateral extensions are 4 mm wide and 12 mm long. The lateral extensions bear last order fertile segments with microsporangia. The microsporangia are fusiform, with acute apices. They form lax clusters consisting of three to five microsporangia per cluster. At the apical part of the fertile frond there are rare isolated microsporangia attached directly to the frond rachis. Size of microsporangia varies from 2–5 mm length and 1–2 mm width. Some microsporangia have curved longitudinal folds probably corresponding to the opening mechanism of adult microsporangia. Same types of microsporangia are known among other groups of Late Palaeozoic pteridosperms (for example, *Permotheca* Zalessky; see for comparison: Naugolnykh 2007: 145, Fig. 67 F, 150, Fig. 68 F, Plate XXXIV, Fig. 8).

Walls of microsporangia are relatively thick, they consist of prolonged cells and are strongly vascularized (Fig. 10 F, G). Vascularization consists of well-developed tracheids of 40–50 µm in diameter, with ringlike and stairlike thickenings (Fig. 10 G). Each microsporangium has up to twelve tracheids in its base reaching from the base to the middle part of the microsporangium.

***In situ* prepollen.** Numerous prepollen grains were extracted from the holotype (No. 4846/148: Fig. 2 D, F, Fig. 3, Fig. 10 A–E) and the syntype (No. 4846/150A: Fig. 2 C, E, Fig. 10 F–H). General morphology of the prepollen enables to assign them to the genus *Plicatipollenites* Lele, 1964, which is regarded as a typically Gondwana taxon (see, for example, Banerjee & D'Rozario 1988) ranging from Carboniferous to Permian, but is also known in other areas of Peri-Thethys (Zavialova & Stephenson 2006) and Siberia (Betekhtina et al. 1988: Plate LXV, Figs 10–11).

Prepollen are round to ovoid, relatively large, up to 60–100 µm in diameter, with a well developed equatorial quasisaccus which often can be detached from the central corpus and preserved separately. Well preserved prepollen grains have a distinct trilete mark at the proximal pole. One of the macerated microsporangia (Fig. 10 F) clearly shows prepollen preserved inside and partly released from its apical part. The trilete scar of the prepollen of *Angaranthus victorii* most probably functioned as an aperture, too, as it has already been suggested for other *Plicatipollenites* prepollen (Zavialova & Stephenson 2006).

Remarks. Among all the specimens studied there are many fragments and two nearly almost complete fronds belonging to the genus *Angaridium* Zalessky. They show a distinct gradual transition from leaves with strongly dissected pinnules (Fig. 2 D right, Fig. 4 D left, Fig. 5 A, C–F, Fig. 6 A, Fig. 7 D–E), to leaves of intermediate morphology (Fig. 5 B, Fig. 7 B–C) and finally to leaves with subtriangular entire-margined pinnules (Fig. 2 F, Fig. 4 A–C, D right, Fig. 6 B, Fig. 7 A). In this particular case, there is no doubt that the fronds with deeply dissected, intermediate and entire-margined pinnules belonged to one and the same natural species. But in the current tradition of Angaran palaeobotany the leaves of *Angaridium* with deeply dissected pinnules are commonly assigned to *A. potaninii* (Schmalhausen) Zalessky (type-species

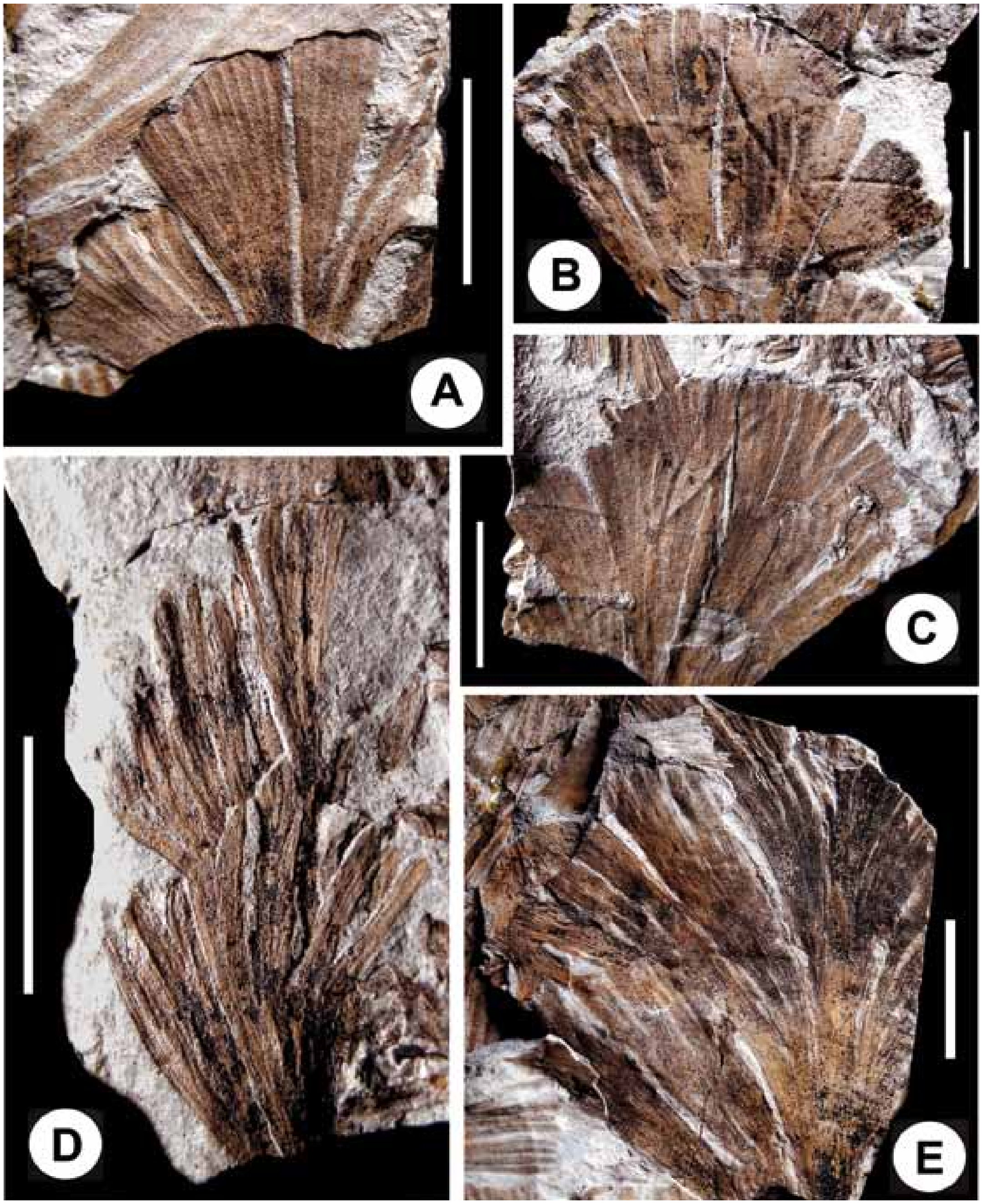

Figure 7. Morphology of sterile leaves of *Angaridium* sp., associated with the male fructifications of *Angaranthus victorii* Naug., sp. nov. A–C – apical parts of the fronds, A – spec. 4846/150e; B – spec. 4846/150b; C – spec. 4846/149c; D – deeply dissected pinnules, spec. 4846/150c; E – near-apical part of the frond, spec. 4846/149d. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars = 1 cm.

of *Angaridium*), the intermediate leaves with polylobate to bilobate pinnules are assigned to *A. submongolicum* Neuburg and leaves with entire-margined subtriangular pinnules are assigned to *A. mongolicum* Zalessky. In fact, all these types often occur together in the same locality and can even be neighboring on the same slab (see here, for example, Fig. 4 D; or Neuburg 1948:

Plate XL, Figs 3–4). Two more species described as *Angaridium finale* Neuburg, 1948, and *A. ignotum* Neuburg, 1948, were established on the basis of insignificant differences and on scarce material, so perhaps they might be regarded as younger synonyms of *A. potaninii*.

Nevertheless, I am not certain that we should treat all of the species listed above to be strict taxonomical synonyms, because despite their considerable similarity they could reflect some local adaptations and therefore could indicate initial phases of sympatric origin of new species. Some cases are known where only one species is recorded from an individual locality. As an example we can mention specimens from the Katskian Formation (Middle Carboniferous) of Tunguska basin (Siberia). Although ascribed to *Angaridium finale* Neuburg, they are very similar to *A. potaninii* (Rasskasova 1962).

The strong taphonomical link between leaves of *Angaridium* and microsporangiate reproductive organs of *Angaranthus victorii* clearly shows that these organs once belonged to one and the same parent plant. Female fronds of *Gondwanotheca sibirica* Neuburg (Fig. 8 B) and seeds of *Angarocarpus ungensis* (Zalessky) Radczenko (Fig. 8 D) most probably also belonged to the same plant (Meyen 1988). Leaves of *Angaridium* and seeds of *Angarocarpus*-type are often found together in close association (see, for example, Zalessky 1918: Plate II, Fig. 4).

Discussion

The general habit and the morphological structure of both sterile leaves and seed-bearing organs of the Angaranthaceae representatives are very similar to those of the Early Carboniferous pteridosperm known as *Lyrasperma scotica* (Calder) Long, reconstructed by Retallack & Dilcher (1988) as a shrubby plant with a monopodial stem and bifurcated fronds. Such bifurcated fronds have not been known for *Angaridium* yet, but leaves of the latter genus have deeply dissected segments, which are almost identical to pinnules of *Sphenopteridium pachyrrachis* (Goeppert) Potonié belonging to the parent plant of *Lyrasperma scotica*, as argued by Retallack & Dilcher (1988). Bicornute seeds of *Lyrasperma scotica* also have many features in common with seeds of *Angarocarpus ungensis* (Zalessky) Radczenko (Fig. 5 D). On the basis of this similarity, we can conclude that Euramerican *Lyrasperma* and Angaran Angaranthaceae are phylogenetically close to each other and belong to the order Callistophytales.

But there is a strong difference between prepollen of *Colatisporites denticulatus* Neville (Neves et al. 1973), known as prepollen of *Lyrasperma scotica* (Retallack & Dilcher 1988) and prepollen of *Plicatipollenites* extracted from the microsporangia of *Angaranthus victorii*. According to my viewpoint, this difference can be explained as a result of evolutionary diversification of the Carboniferous Callistophytalean pteridosperms which grew in different palaeophytogeographical realms and were adapted to different climates.

The leaves, which are very similar to the leaves of *Angaridium*, are known from the Lower Carboniferous deposits of Gondwana and were attributed to the genera *Nothorhacopteris*, *Triphyllopteris*, *Sphenopteridium* (see, for example, Januzzi & Pfefferkorn 2002: Fig. 4 C–E). The leaves of similar shape are associated with the seeds of *Eonotosperma arrondoi* Césari, described from the Lower Carboniferous of Argentina (Césari 1997). There are some Carboniferous microsporangiate fructifications of pteridosperms in Gondwana described as *Obandotheca laminensis* (Erwin et al. 1994), which are similar to *Angaranthus victorii* in the general organization

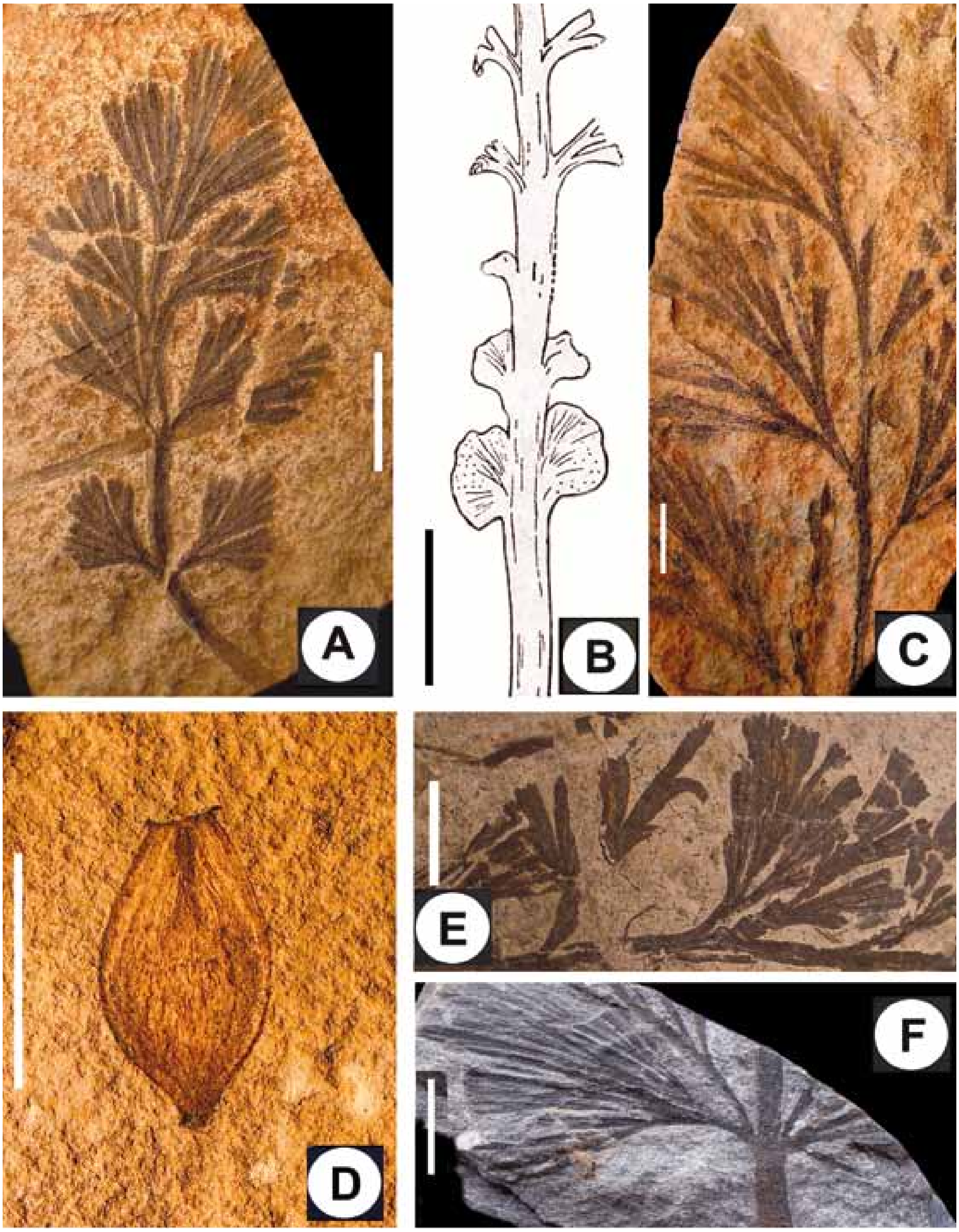

Figure 8. Different representatives of Angaranthaceae Naug., fam. nov. A – *Angaridium potaninii* (Schmalhausen) Zalessky, complete young sterile frond, Tarbagatai, Talagoi Range, right bank of the Taidzhuzgen River (same specimen figured in Zalessky 1918: Plate I, Fig. 11); B – *Gondwanotheca sibirica* Neuburg, basal part of the female (seed-bearing) reproductive organ, Alykaevskaya Formation, left bank of the Severnaya Unga River, downstream Cheremichkina village (after Neuburg 1948: Plate XXXVIII, Fig. 5, 5a); C – *Angaridium potaninii* (Schmalhausen) Zalessky, almost complete well-developed sterile frond, Tarbagatai, Talagoi Range, right bank of the Taidzhuzgen River (same specimen figured in Zalessky 1918: Plate I, Fig. 5); D – *Angarocarpus ungensis* (Zalessky) Radczenko, an isolated seed, Kuznetsk Basin, left bank of the Unga River, downstream of the Cheremychkina village (same specimen figured in Zalessky 1918: Plate LI, Fig. 9); E – *Angaridium potaninii* (Schmalhausen) Zalessky, middle part of the well >>

of their fertile organs (compare: Erwin et al. 1994: Fig. 4b and Fig. 9 in the present paper), but different in their combination of microsporangia in small but distinctly compact clusters consisting of two up to four microsporangia.

The Middle Carboniferous floristic assemblage of Angaraland, which is provisionally called here the 'Mazurovskian floristic assemblage', includes an admixture of typically Angaran endemic taxa and those taxa which could be regarded as migrants from Euramerica or widely spread cosmopolitan taxa. Typically Angaran elements of the Mazurovskian assemblage include lycopods like *Angarodendron obrutschevii* Zalessky emend. Meyen; equisetophytes like *Koretrophyllites mungaticus* Radczenko, *K. vulgaris* Radczenko, *Phyllotheca tomiensis* Chachlov, *Paracalamites crassus* Gorelova, *P. mrassiensis* Radczenko; ferns like *Sphenopteris bellatula* Zalessky; pteridosperms of Angaranthaceae affinity like *Abacanidium abaeanum* (Zalessky) Radczenko, *Angaropteridium cardiopteroides* (Schmalhausen) Zalessky, *A. tyrganicum* Zalessky; true pteridosperms of Angaranthaceae like *Angaranthus victorii* Naugolnykh, *Gondwanotheca* sp., *Angarocarpus ungensis* (Zalessky) Radczenko, *Angaridium potaninii* (Schmalhausen) Zalessky, *A. submongolicum* Neuburg, *A. mongolicum* Zalessky, *A. finale* Neuburg, *A. ignotum* Neuburg, *Paragondwanidium petiolatum* (Neuburg) Meyen, *P. sibiricum* (Petunnikov) Meyen; putative zamiopterids (versus peltasperms) like *Pursongia asiatica* Zalessky; early vojnovskyaleans like *Rufloria subangusta* (Zalessky) Meyen, *R. theodorii* (Tschirkova et Zalessky) Meyen, *R. tomiensis* (Radczenko) Meyen, *R. tschirkovae* (Zalessky) Meyen, *Rufloria* spp., *Krylovia sibirica* Chachlov (= *Samarospadix penicillata* Neuburg); and isolated seeds like *Rhabdocarpus* (?) *tomiensis* Zalessky, *Cordaicarpus tomiensis* Radczenko, *Samaropsis siberiana* Zalessky, *S. mungatica* Neuburg, *S.* (?) *angarica* Rasskasova, *Cardiocarpus krivljakiensis* Suchov, *Holcospermum* (?) *tchelchetensis* Suchov (Neuburg 1948; Meyen 1972, 1976; Betekhtina et al. 1988; Budnikov & Gorelova 1996; this paper).

The Euramerican migrants or cosmopolitan taxa include bowmanitids (sphenophylls) like *Sphenophyllum denticulatum* Zalessky (very close if not synonymous to *Sphenophyllum majus* Bronn; for comments see Neuburg 1948: 64–66, Plate IX, Figs 1–9, 11) and the trigonocarpalean pteridosperms *Neuropteris izylensis* (Tschirkova) Neuburg, *N. siberiana* Zalessky and *N. tomiensis* (Zalessky) Radczenko (endemic formal species of neuropterids, although very similar to several typically Euramerican species).

This admixture of endemic and Euramerican components in the Mazurovskian floristic assemblage strongly supports the idea of a direct relationship between Europe and Northern China, which took place in the end of Early Carboniferous and Middle Carboniferous (Laveine et al. 1989). The southern part of Siberia in Carboniferous was part of the migration path from Europe to Northern China and was also affected by back-migrations from Cathaysia at the times of optimum climatic condition, when warm-like thermophilic floristic elements (for example, bowmanitids and neuropterids) could invade into southern areas of Angaraland. Very similar migration processes took place in that region during the Permian (Yang et al. 2011; Leven et al. 2011).

<< developed frond, Tarbagatai, Talagoi Range, right bank of the Taidzhuzgen River (same specimen figured in Zalessky 1918: Plate I, Fig. 10); F – *Rhodea javorskii* Radczenko, Lower Carboniferous, Ostrog Formation, Kuznetsk basin, right bank of Tom River, upstream from the Kameshok village, TsNIGR Museum 131(85)/9259, G. P. Radczenko collection. Scale bars = 1 cm.

Figure 9. A – reconstruction of female reproductive organ *Gondwanotheca sibirica* Neuburg; B – reconstruction of male reproductive organ *Angaranthus victorii* Naug., sp. nov. Middle Carboniferous, Siberia. Scale bar = 1 cm.

Nonetheless, some stenobiontic endemic groups of higher plants, such as the family Angaranthaceae, originated independently in Angaraland and were characteristic of that region in the Middle Carboniferous without any further migrations to the south-east (with the exception of Kazakhstan and adjacent areas of Middle Asia) or to the west, which most probably was controlled by climatic conditions and strict ecological adaptations of these plants.

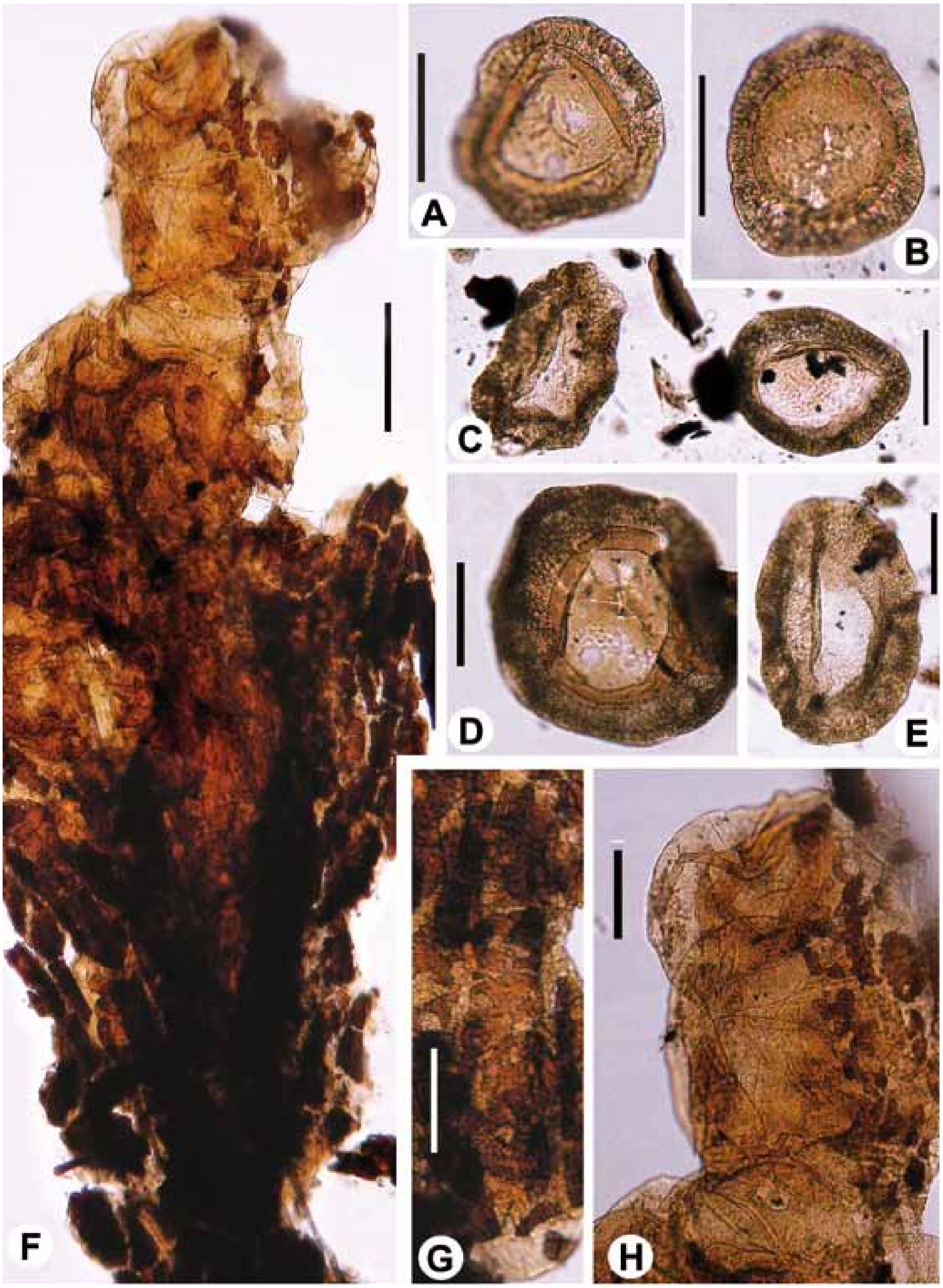

Figure 10. Morphology of prepollen of *Plicatipollenites* sp., which were preserved *in situ* in microsporangia of *Angaranthus victorii* Naug., sp. nov. (A–E, H), a microsporangium with well preserved base and with the numerous prepollen of *Plicatipollenites* sp., preserved *in situ* (F), and a tracheid from the wall of the microsporangium (G). A–E – holotype 4846/148a; F–H – syntype 4846/150A. Kansk locality, the right bank of Kan River, near eastern part of Kansk, near mouth of Mohovoi Rivulet; Middle Carboniferous, Listvjazhninskaya Formation. Scale bars: A–E, G, H = 50 µm; F = 100 µm.

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