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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

Serge V. Naugolnykh

Summary: The paper deals with the emendation and morphological reinterpretation of *Quasistrobus ramiflorus* Vladimirovich, emend. nov., which was initially misinterpreted by the author of these genus and species as a conifer. Now is classified to the family Angaropeltaceae belonging to the order Peltaspermales. Detailed data on the seed-bearing organs of *Quasistrobus ramiflorus*, its leaf morphology, associated seeds, microsporangiate polliniferous organs and anatomy of leaves are given. Some aspects on supposed entomophily of angaropeltian pteridosperms are discussed.

Keywords: Gymnosperms, peltasperms, evolution, Permian, Wordian, entomophily

The main tendencies and trends in evolution of advanced gymnosperms have always been and still are actual in palaeobotanical research, because they can be used as a valuable basis for proper understanding of causes resulted in the appearance of angiosperms and reflected in the process, which is often cited as 'angiospermisation' now (Ponomarenko 1996). One of the most important components of this process was the origin of the semi-closed or practically completely closed seed-bearing capsules, which took place during the Permian period in various representatives of the gymnosperms belonging to the family Angaropeltaceae Doweld emend. Naugolnykh, i.e. in the advanced peltasperms.

The most ancient representatives of this family are found in the lower Permian deposits (namely Kungurian) of the Urals, Russia. They belong to two closely related genera, *Sylvocarpus* Naugolnykh and *Permoxylocarpus* Naugolnykh, which are associated with long linear or lanceolate leaves with parallelodromous venation formed by dichotomizing (isotomizing) veins furcated mostly in the basal part of the leaf.

In Roadian and Wordian time (i.e. in Ufimian and Kazanian consequently, according to traditional Russian stratigraphical nomenclature), the early angaropeltians gave rise to the genus *Angaropeltum* Doweld (nomenclatorial variant for the genus *Cardiolepis* Neuburg emend. S. Meyen; see for further references: Doweld 2001) linked with the leaves of the genus *Phylladoderma* Zalessky (Zalessky 1914) and closely related taxa such as *Sardykphyllum* Zalessky (Zalessky 1929), which are very characteristic for these deposits in Angaraland. The type of attachment of the seed-bearing capsules of *Angaropeltum* to the fertile shoots or branches is still unknown.

Besides the genus *Angaropeltum*, some other genera with special adaptive structures aiming protection of the ovules were described from the Permian and Triassic deposits of Russia and attributed to a new peltasperm family Vetlugospermaceae (Naugolnykh 2012).

The present paper is devoted to the emendation and detailed description of an angaropeltian plant, which is known as *Quasistrobus ramiflorus* Vladimirovich (initial manuscript description:

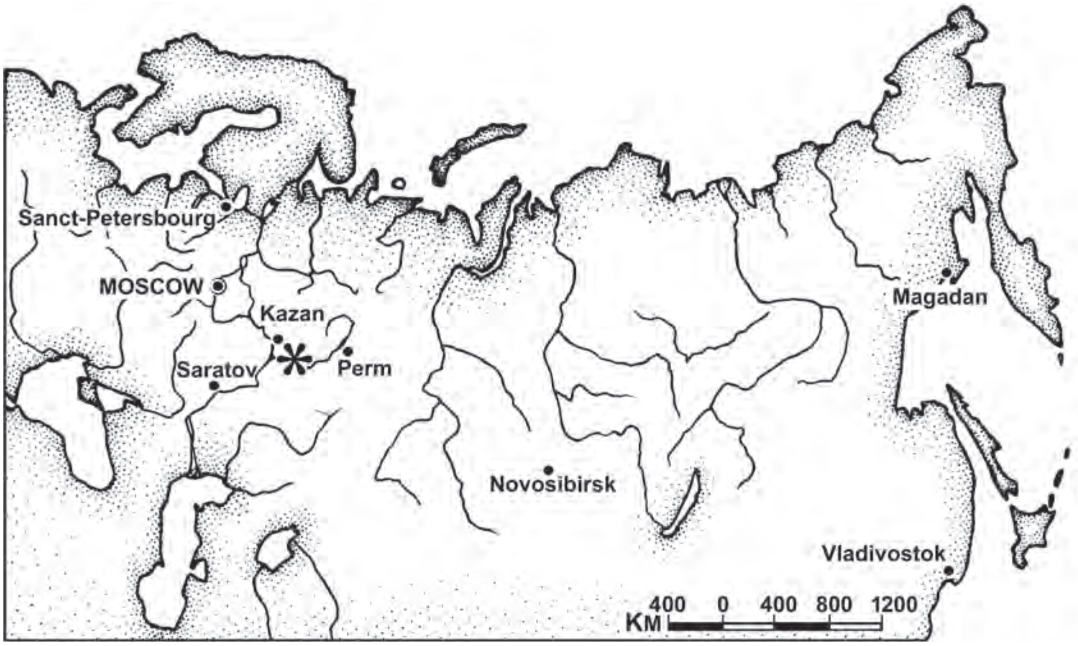

Figure 1. Geographical and stratigraphical position of the Tarlovka locality (marked by an asterisk).

Vladimirovich 1984; validation of the taxon: Vladimirovich 1986). This plant is practically ignored in the current paleobotanical literature, mainly because it was completely misinterpreted in the protologue.

Materials and methods

The collection studied is kept at the Central Scientific-Research Geological Museum named after Tschernyshev in Saint-Petersburg, Russia. Several additional specimens from the author's collection (*Sylvocarpus* seed-bearing capsules and *Praephylladoderma* leaves) were used as comparative material as well.

The compressed plant material was macerated in concentrated nitric acid for a week, then the products of oxidation were removed by ammonia solution. The cuticles obtained were washed in distilled water, dried up and studied in optic microscope PZO with interference contrast and in scanning electron microscope (Vega Tescan MV 2300 SEM at the Geological Institute of the Russian Academy of Sciences, Moscow).

The collection studied includes nine fertile shoots preserved to different extents and four sterile leafy shoots. All of them were found together in the same sandstone concretion, taphonomically buried together and probably belonging to the same individual parent plant. All of the *Quasistrobus ramiflorus* specimens originated from the same locality Tarlovka (Fig. 1).

This locality is often cited in palaeobotanical and stratigraphical works about the Middle Permian deposits of the Volga River basin (review in Esaulova 1986), but only one detailed stratigraphical column/log with layer-by-layer description has been published so far (Tsymbal 2012).

The generalized stratigraphical column of the Tarlovka locality published by Esaulova (1986: 32, Fig. 6, outcrop 14) and the detailed Tarlovka column published by Tsymbal (2012: 87, Fig. 1) are basically similar. Both columns show dominance of sandy clastic material in the middle part of the outcrop, and the sandstone lenses and coals with the plant megafossils were disposed just above the sandy part of the stratigraphical succession. The integrative list of the plant taxa reported by Vladimirovich (1984; based on the collection of V.P. Gorsky, who visited the Tarlovka locality in 1971), Esaulova (1986) and Tsymbal (2012) with the nomenclatorial innovations added and edited by the present author, includes the following species: lycopodiophyte *Signacularia noinskii* Zalessky, its phylloids *Viatscheslaviophyllum kamiense* Esaulova and megaspores *Laevigatisporites* sp.; equisetophytes s. l. *Paracalamitina striata* Zalessky emend. Naug., *Paracalamites kutorgae* (Geinitz) Zalessky, *Paracalamites* sp., *Annularia stellatoides* Neuburg, *A. kamiensis* Vladimirovich, bowmanitids *Sphenophyllum stoukenbergii* Zalessky; ferns *Corsinopteris petschorica* (Fefilova) Doweld emend. Naugolnykh (taxonomical status of this species is discussed in Naugolnykh 2013); *Pecopteris anthriscifolia* (Goeppert) Zalessky, *P. kazanica* Vladimirovich, *P. obtusa* Radczenko, *Lobatopteris* sp., *Prynadaeopteris minuta* Vladimirovich, *P. rhomboidea* Vladimirovich; pteridosperms s.l. *Permocallipteris wangenheimii* (Fischer) Naug. (= *Odontopteris rossica* Zalessky; = *O. tatarica* Zalessky: for the morphological concept of the species *Permocallipteris wangenheimii* and basis for synonymy see Naugolnykh 2014; further discussion on the peltasperm leaf taxa see Zhang et al. 2012), *Peltaspermum* sp., *Compsopteris salicifolius* (Fischer) Naug., *Zamiopteris subglossopteroides* Zimina, *Quasistrobus ramiflorus* Vladimirovich emend. nov., *Phylladoderma meridionalis* S. Meyen, *Nucicarpus tarlovskiensis* Esaulova, *N. minutus* Esaulova; ginkgophytes *Rhipidopsis ginkgoides* Schmalhausen, *Sphenobaiera* sp., *Psygmophyllum nesterenkoi* (Zalessky) Burago; conifers *Pseudovoltzia cornuta* S. Meyen, *Pseudovoltzia* sp., *Ullmannia bronnii* Goeppert; vojnovskyopsids *Rufloria* sp., ‘*Cordaites*’ *sylovaensis* (Neuburg) S. Meyen, *Sylvella* aff. *alata* Zalessky, *S. magna* Vladimirovich, *S. heteromorpha* Esaulova, *Bardocarpus elegans* Esaulova, *Entsovia* sp.; isolated seeds of uncertain affinity *Samaropsis* aff. *macroptera* Naug., *Cordaicarpus arensis* Zalessky, *C. gusevii* Vladimirovich.

Vladimirovich (1984) reported on some more plant taxa from the same locality, but their attribution seems dubious: *Tudrodendron tatarica* Vladimirovich (most probably an untypical form of preservation of *Signacularia noinskii* Zalessky), *Cladophlebis kamiensis* Vladimirovich (younger synonym of *Pecopteris helenaeana* Zalessky) and *Tatarina* sp. (fragment of the pinnae belonging to *Psygmophyllum* sp.). The holotype of putative ginkgophyte *Flabellosemen riparium* Tsymbal also originated from the same locality (Tsymbal 2014), but this material needs a revision. Most probably, this species should be reassigned to the genus *Cheirocladus* Naug., which was proposed for ginkgophytes with *Psygmophyllum*-type leaves (Naugolnykh 2007). Stratigraphically, the Tarlovka locality belongs to the lower part of the Upper Kazanian substage, the Kamyshla layers (Esaulova 1986), i.e. to Wordian according to the modern stratigraphical nomenclature.

Systematic treatment

Class Peltaspermopsida Cronquist, 1981

Order Peltaspermales Taylor, 1981

Family Angaropeltaceae (Doweld, 2001) Naugolnykh, 2012

Quasistrobus Vladimirovich, 1986, emend. Naugolnykh, emend. nov.

Synonymy. *Quasistrobus* Vladimirovich, 1986: 36.

Type species. *Quasistrobus ramiflorus* Vladimirovich, 1986; Middle Permian, Wordian (Kazanian), the Volga River basin.

Original diagnosis (after: Vladimirovich 1986; translated by S. Naugolnykh. The diagnosis is captioned as 'description' in the protologue.). "Sterile stems simple. Leaves spiral, simple sessile, dimorphic. Fertile stems are lax aggregation of micro(?)strobili, which originate spirally directly on the axis of the stem alternating with vegetative leaves. Micro(?)strobili radially-symmetrical, funnel-like, on naked stalk. Micro(?)sporophylls considerably reduced. Sporangia trailing (pendulate)."

Emended diagnosis. Female reproductive organs (megasporophylls) peltate, forming seed-bearing capsules. Each capsule includes eight ovules in average. Margins of capsules lobate after capsule being adult and open. Seed scars (ovule scars) are disposed near central stalk of capsule and located in a circle around the stalk. Capsules are attached to fertile stem and form the fertile zone. Seed-bearing capsules are intercalated with sterile leaves. Sterile leaves are linear to lanceolate, with parallelodromous venation. Male reproductive organs (polliniferous organs) consist of fusiform sporangia fused at bases.

Comparison. The main differences between the genera *Quasistrobus* Vladimirovich, emend. nov., and the closely related *Sylvocarpus* Naugolnykh (Naugolnykh 2008) are: (1) presence of the sterile leaves between the seed-bearing capsules of *Quasistrobus* and (2) proliferation of the shoot through the fertile zone of *Quasistrobus.*

Distribution. Middle Permian, Wordian (Kazanian); Western Angaraland (eastern part of the European Russia and the Urals).

Quasistrobus ramiflorus Vladimirovich, 1986, emend. nov., Figs 2–7, 9

Synonymy. *Quasistrobus ramiflorus* Vladimirovich, 1986: 36, Plate 153, Figs 2, 3.

Holotype. No. 10/122330, TsNIGR-Museum, Saint-Petersburg; Tarlovka locality, Wordian (Kazanian), Kamyshla layers; figured here on Figs 4 A; 5 A–G; 6 A–G; 7 A–E.

Description. General characteristics: the plant under consideration had peltate seed-bearing capsules of spherical shape, when the capsules were young and undeveloped. The capsules became flattened in maturity and after dissemination of seeds. Average diameter of the seed-bearing capsules after dissemination varies from 7 to 8 mm. The seed scars are round to ovoid, 1–1.5 mm in diameter. The radially arranged resin channels (ducts) and ovoid resin bodies are present in the walls of the seed-bearing capsules. The seed scars are disposed in a circle around the central stalk of the seed-bearing capsule. The central stalk is well-developed, up to 7 mm long. The seed-bearing capsules are disposed on the axis in spiral order, and form more or less compact fertile zones consisting of twenty capsules at least. The seeds/ovules are of ovoid shape, with a wide obtuse base and more or less acute apex (micropylar part). The seed-bearing capsules alternate with sterile lanceolate leaves located between neighboring capsules. The sterile leaves of *Phylladoderma* or *Sardykphyllum*-type are lanceolate to needle-like with a somewhat attenuate base. The simple vein comes from the leafy shoot or from the axis of the fertile shoot/fertile zone into the leaf base. Polliniferous organs are synangiate aggregations of fusiform or clavate microsporangia of *Permotheca*-type, consisting of four or more microsporangia (Fig. 3E). The microsporangia are attached to the common base and slightly fused at their proximal parts.

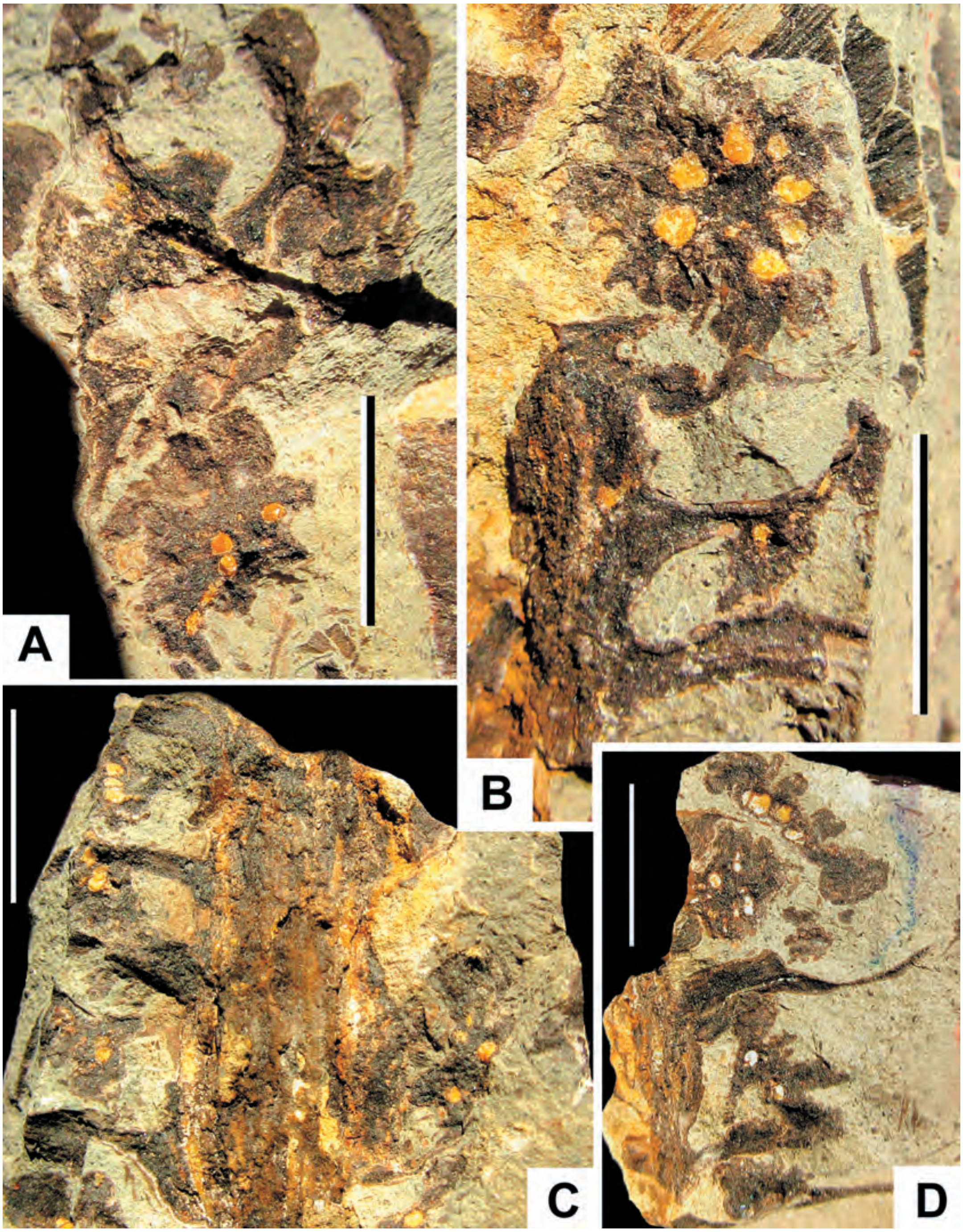

Figure 2. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. Morphology of the fertile shoots. Specimens: A – 34/12271; B – 34/12271; C – 31/12271 (counterpart of spec. 35/12271); D – 43/12271. Middle Permian, Wordian (Kazanian); Tarlovka locality. Scale bars = 1 cm (A–D).

All the specimens attributed to this species originate from one and the same locality, and moreover, from one and the same slab, and therefore might represent one and the same parent plant. This estimation can be illustrated by the specimens showing natural connection of the fertile shoots, seed-bearing capsules and sterile leaves attached to the axis (Figs 2A–D; 3B; 4A)

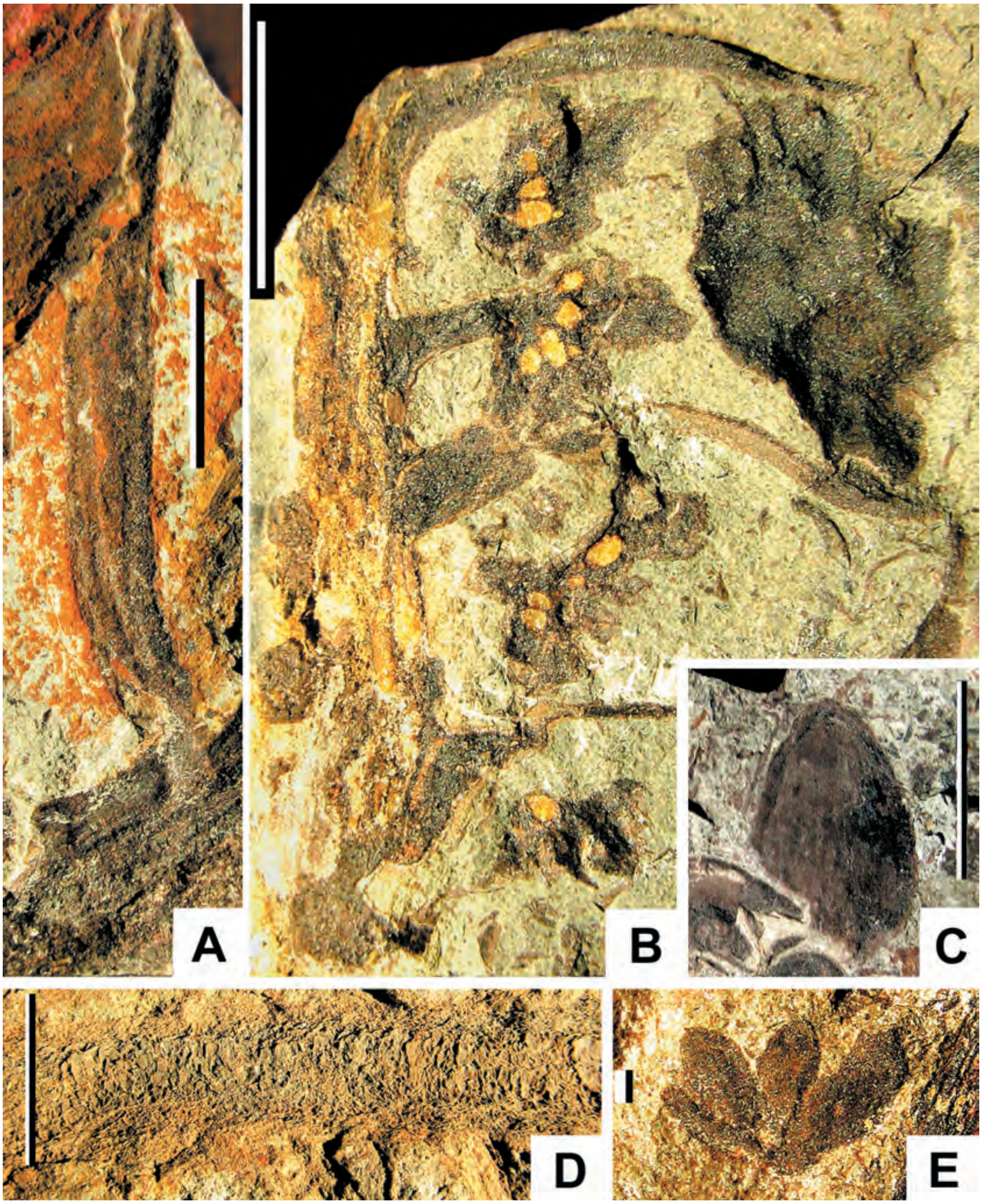

Figure 3. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. A – morphology of the sterile leaf of *Phylladoderma*-type; B – fertile shoot with opened seed-bearing capsules; C – seed found in close association with the fertile shoot of *Quasistrobus ramiflorus*; D – axis with cross striation; E – male synangiate organ of *Permotheca*-type found in close association with the fertile shoot of *Quasistrobus ramiflorus*. Specimens: A – 35/12271; B – 35/12271; C – 9/12230; D – 36/12271; E – 35/12271. Middle Permian, Wordian (Kazanian); Tarlovka locality. Scale bars = 1 cm (A–D), 1 mm (E).

and by the close association of all the specimens. One more reason for uniting or combining seed-bearing capsules, sterile leaves and polliniferous organs into one and the same taxon of practically natural ('botanical') status is a direct extrapolation with the other representatives of

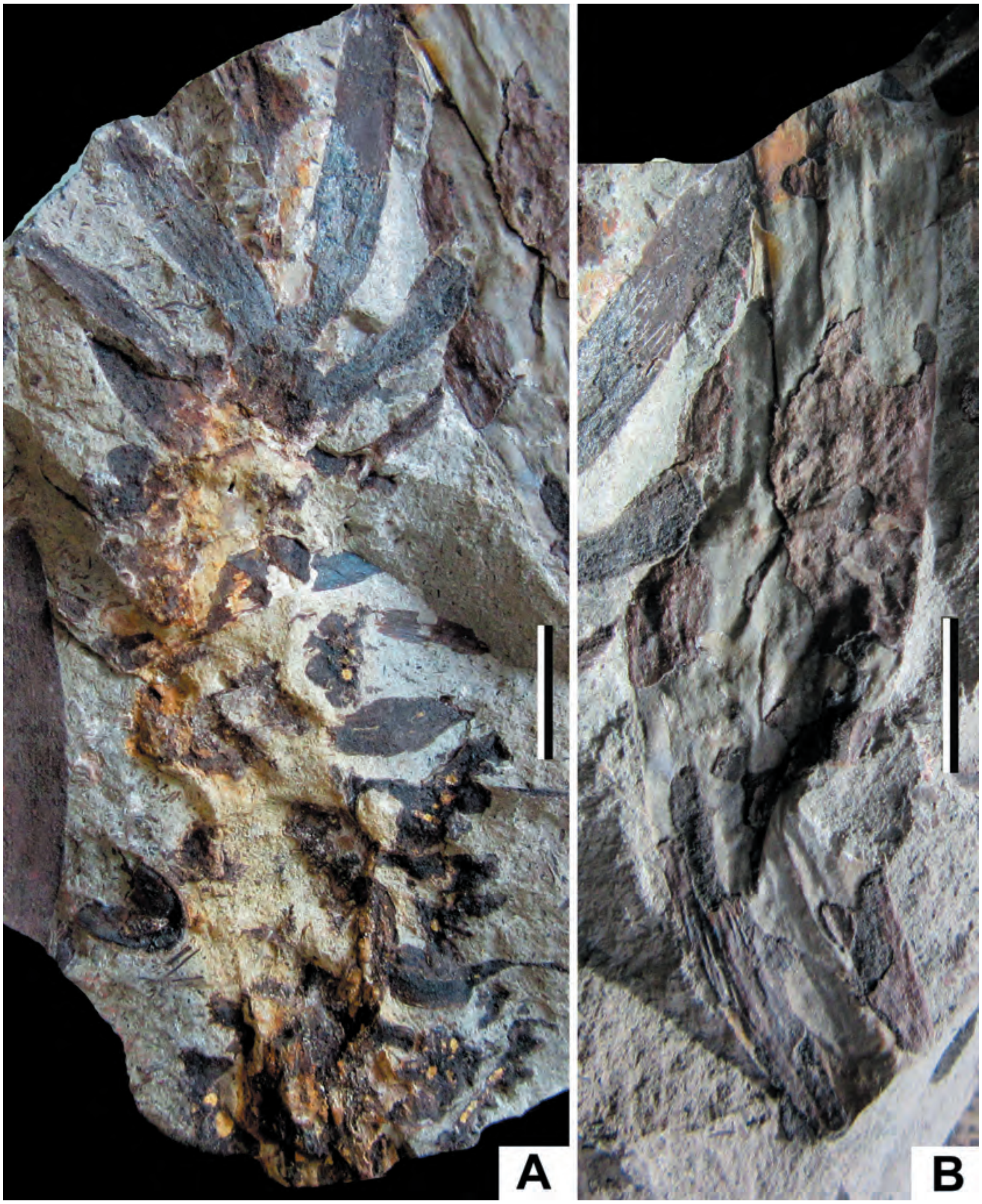

Figure 4. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. A – Holotype of the species: 10/12230, a fertile shoot with the lanceolate leaves intercalating with the seed-bearing organs; B – *Phylladoderma*-like lanceolate leaves found in close association with the fertile shoot of *Quasistrobus ramiflorus* on the same slab. Middle Permian, Wordian (Kazanian); Tarlovka locality. Scale bars = 1 cm (A–B).

the family Angaropeltaceae, i.e. *Angaropeltum* Doweld (seed-bearing capsules), *Phylladoderma* (sterile leaves) and *Permotheca*-like polliniferous organs (Meyen 1982). One more extrapolation model is the co-occurrence of seed-bearing organs of *Permoxylocarpus* Naugolnykh and the leaves of *Praephylladoderma* Naugolnykh in the Lower Permian (Kungurian) deposits of the Cis-Urals (Naugolnykh & Oskolski 2010).

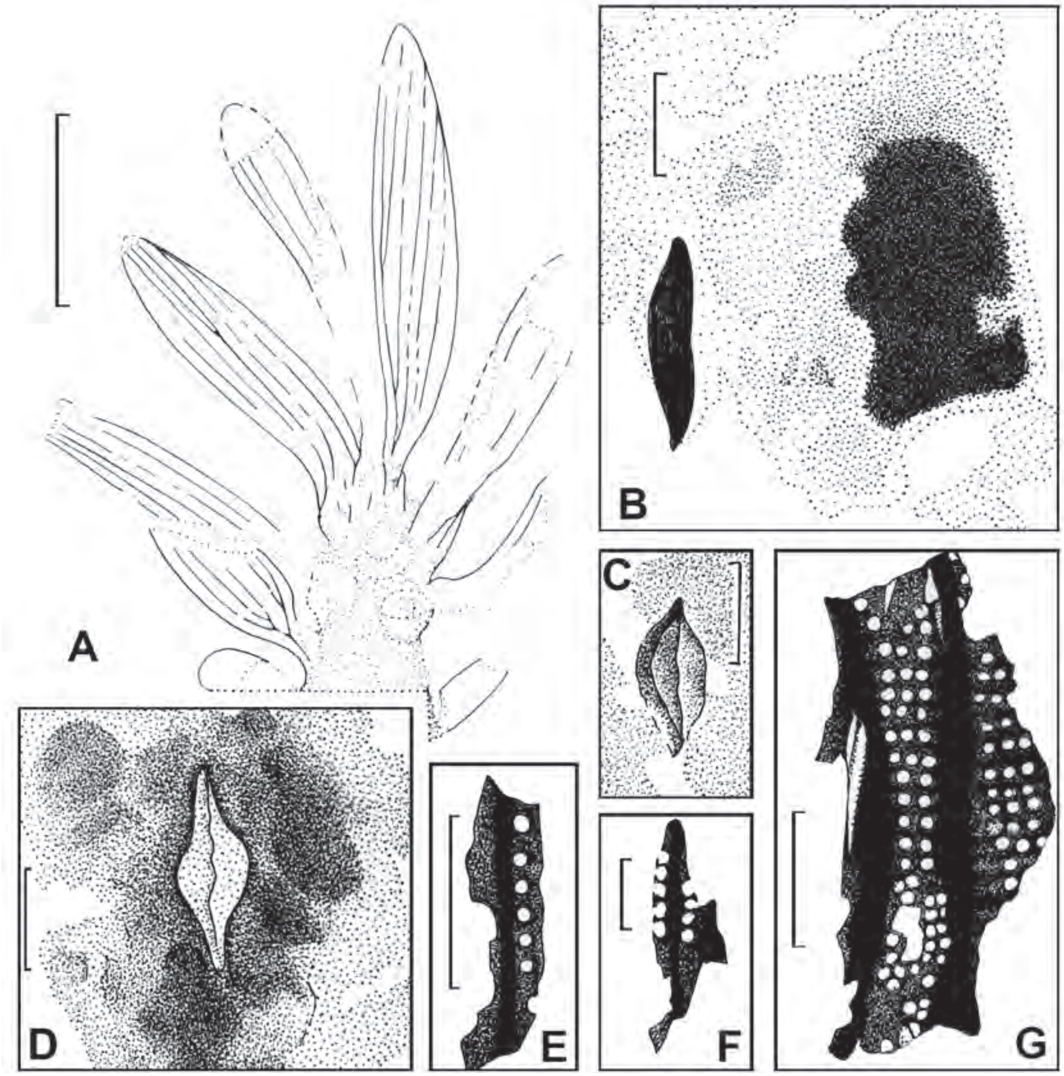

Figure 5. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. Tracing line-drawings after the cuticle preparations, which were taken from the leaf of the terminal leaf bunch of the holotype 10/12230. A – interpretative morphology of the terminal leaf bunch; B – resin duct; C, D – stomata; E, F, G – conductive tissues. Middle Permian, Wordian (Kazanian); Tarlovka locality. Scale bars = 1 cm (A); 50 µm (B–G).

The most important feature of *Quasistrobus ramiflorus* is the structure of the seed-bearing capsules, which were misinterpreted in the protologue as male reproductive organs (Vladimirovich 1986). There are two principal modes of preservation of seed-bearing capsules in the collection studied, i.e. (1) flattened open capsules preserved on the bedding plane of sedimentation with the stalk orientated across the bedding plane (Fig. 2B), and (2) when the seed-bearing capsule lies on its side showing the stalk in almost all its length (Fig. 2A, upper seed-bearing capsule; Fig. 3B, a capsule at the center of the picture). There are also some combined modes of preservation, when the seed-bearing capsules are visible as flattened, but the stalk is also visible. Two 'seeds'/'ovules' figured by Vladimirovich (1984, Plate VII, Fig. 8; Plate IX, Fig. 5) could be interpreted as closed, undeveloped juvenile seed-bearing capsules, but it is not possible to prove this conclusion, because of insufficient preservation of this specimen (36/12271).

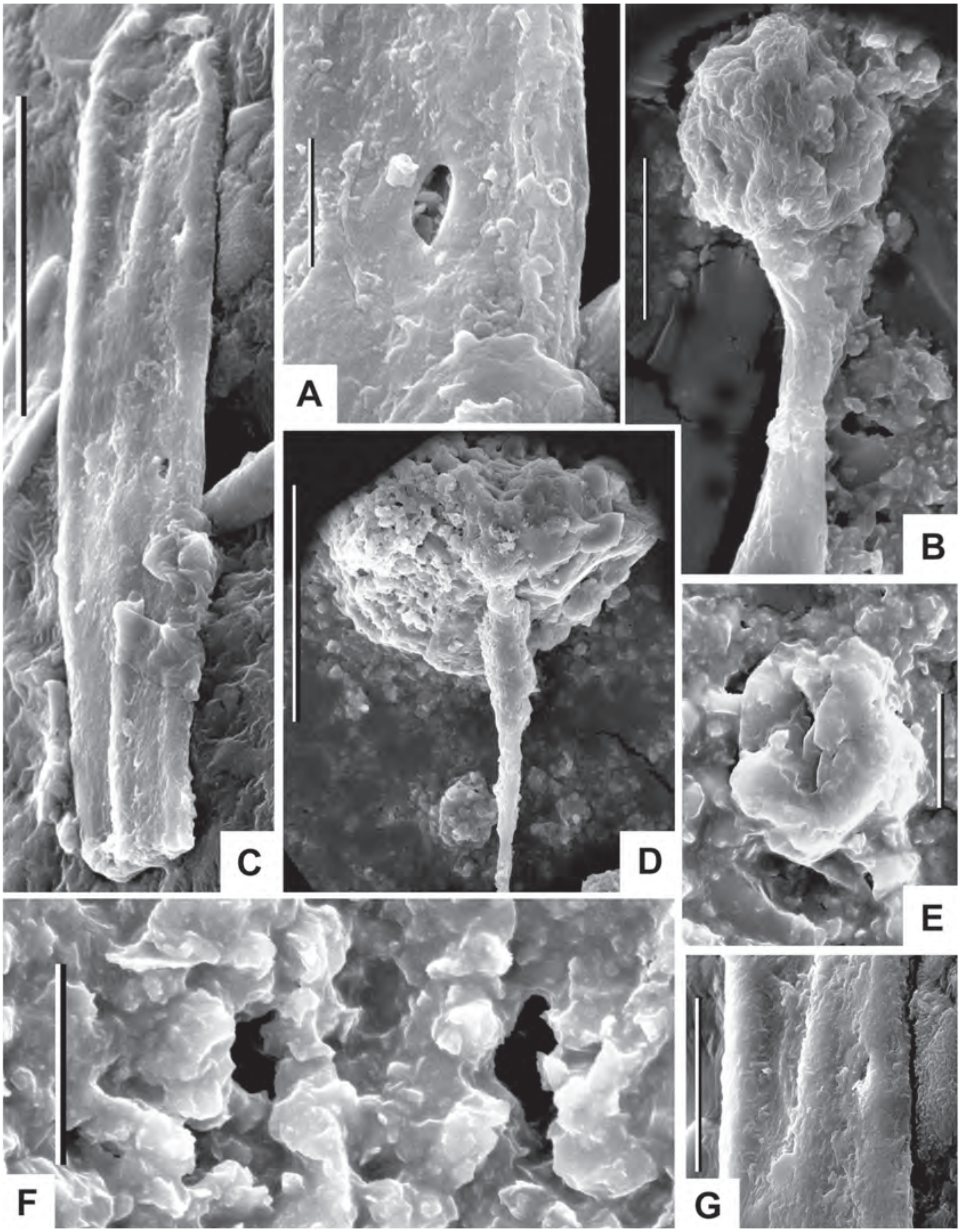

Figure 6. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. Anatomical structure of the leaf from the terminal leaf bunch of the holotype 10/12230. A – pit pore in the tracheid wall; B, D – resin ducts ending in ovoid resin bodies; C, G – tracheids; E – stoma; F – outer surface of the cuticle. Middle Permian, Wordian (Kazanian); Tarlovka locality. Scale bars = 5 µm (A); 10 µm (E, F); 20 µm (B, D, G); 50 µm (C).

As far as we can judge from the most complete specimens (Figs 3B; 4A), the seed-bearing capsules were attached to the fertile shoot or axis of the fertile zone in spiral order. Vertical distance between neighboring capsules is about 5 mm in average. Some of the shoots bear characteristic

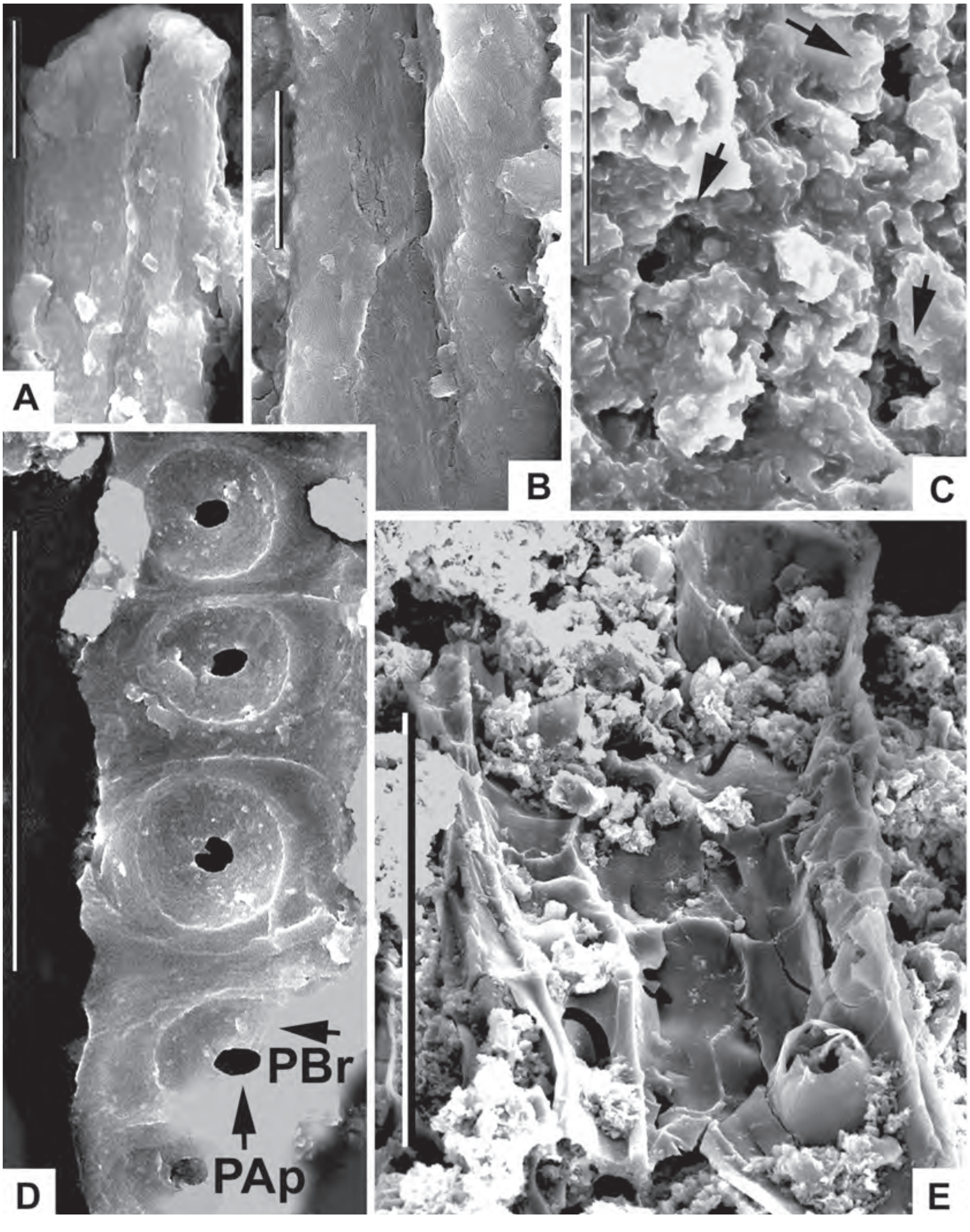

Figure 7. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. Anatomical structure of the leaf from the terminal leaf bunch of the holotype 10/12230. A, B – tracheids; C – outer surface of the cuticle, the stomata are marked by the arrows; D – tracheid with the bordering pits (PBr – pit border or secondary wall; PAp – pit aperture, the pit membrane inside is not preserved); E – inner surface of the cuticle, one stoma is observed in right lower corner of the photograph. Middle Permian, Wordian (Kazanian); Tarlovka locality. Scale bars = 10 µm (A, B); 20 µm (C); 50 µm (D); 100 µm (E).

cross ribs in the axial part (Fig. 3D). In some cases, sterile leaves are observed between the seed-bearing capsules (Figs 2D; 3B). Shape of the sterile leaves varies from more or less linear, close to the flattened, needle-like structure (Fig. 2D) to leaves of distinct lanceolate shape (Figs 3A;

4A). Venation of the leaves is parallel in general, with a single vein entering the leaf base, and then once or twice dichotomizing.

Several isolated seeds/ovules were found in close association with the seed-bearing capsules (Fig. 3C). Although the seeds were not found in direct natural attachment to the seed-bearing capsules, it is highly possible that they belonged to the same parent plant, because (1) there are no any other seed-bearing organs either seeds in this slabs for suggestion any other combination; (2) these seeds are very similar both in size and shape to the seeds, which are characteristic of other representatives of Peltaspermales (Meyen 1987).

Several cuticle preparations were made from the leaf belonging to a terminal leaf bunch of the holotype 10/12230 (Figs 4A; 5A). The preparations show the cuticle fragments with the narrow stomata (Figs 5C, D; 6E, F; 7C, E). Outer surface of the cuticle is covered by ridge-like papillate outgrowths (Figs 6F; 7C). The surface papillae are of irregular shape, normally about 3–5 µm in diameter. The stomata are deeply sunken, with the thick lip-like guard-cells observed only from the inner surface of the cuticle (Figs 6E, 7E). Common epidermal cells are visible only on the inner surface of the cuticle (Fig. 7E). These cells are more or less ovoid to rectangular. Average size of the cells is 20 × 40 µm. There are numerous resin ducts and bodies. The resin ducts are of fusiform shape (Fig. 5B, left) or can be represented by resin channels (Fig. 6B, D), which end in ovoid resin bodies. Size of the resin bodies in largest dimension varies from 20 to 25 µm or somewhat more. Sometimes dispersed resin-containing tissues of mesophyll origin are observed as well (Fig. 5B, right).

Several tracheids were obtained together with the cuticle fragments (Figs 5E–G; 6A, C, G; 7A, B, D). The tracheids are represented by more or less simple forms with solitary pores in the walls (Figs 6A, C, G) and well-formed tracheids with bordered pore-pairs (Figs 5E, F, G; 7D). Average diameter of the tracheids varies from 15 to 20 µm.

Discussion

First considerations on the relationship between Peltaspermaceae and Angaropeltaceae (former Cardiolepidaceae) were published by Meyen (1988: 356):

> "All the organs of the Cardiolepidaceae contain resin bodies or ducts. The same ducts are observed in axes accompanying *Phylladoderma* leaves in the Kazanian of the Kama River region. These axes bear helically arranged appendages also characterized by resin ducts. Sometimes the appendages are crowned by peltoids with seed scars. Similar fructifications were described by Vladimirovich (1984) as *Quasistrobus ramiflorus*. Some of the fructifications accompanying *Phylladoderma* were probably open peltoids, not semiclosed capsules like *Cardiolepis*. It is also possible that these racemose aggregations of peltoids belong to plants with *Odontopteris rossica* fronds, although in the latter the resin bodies have never been observed. In any case, the close relationship between the Cardiolepidaceae and Peltaspermaceae is evident."

Although this estimation indicates clearly the direct link between Peltaspermaceae and Angaropeltaceae, any detailed scenario of the origin of Angaropeltaceae is not evident judging from Meyen's sentence cited above. Even the most ancient representatives of Peltaspermaceae demonstrate a tendency for curving downwards of the seed-bearing disc margins (Meyen 1987; DiMichele et al. 2005; Fig. 1C).

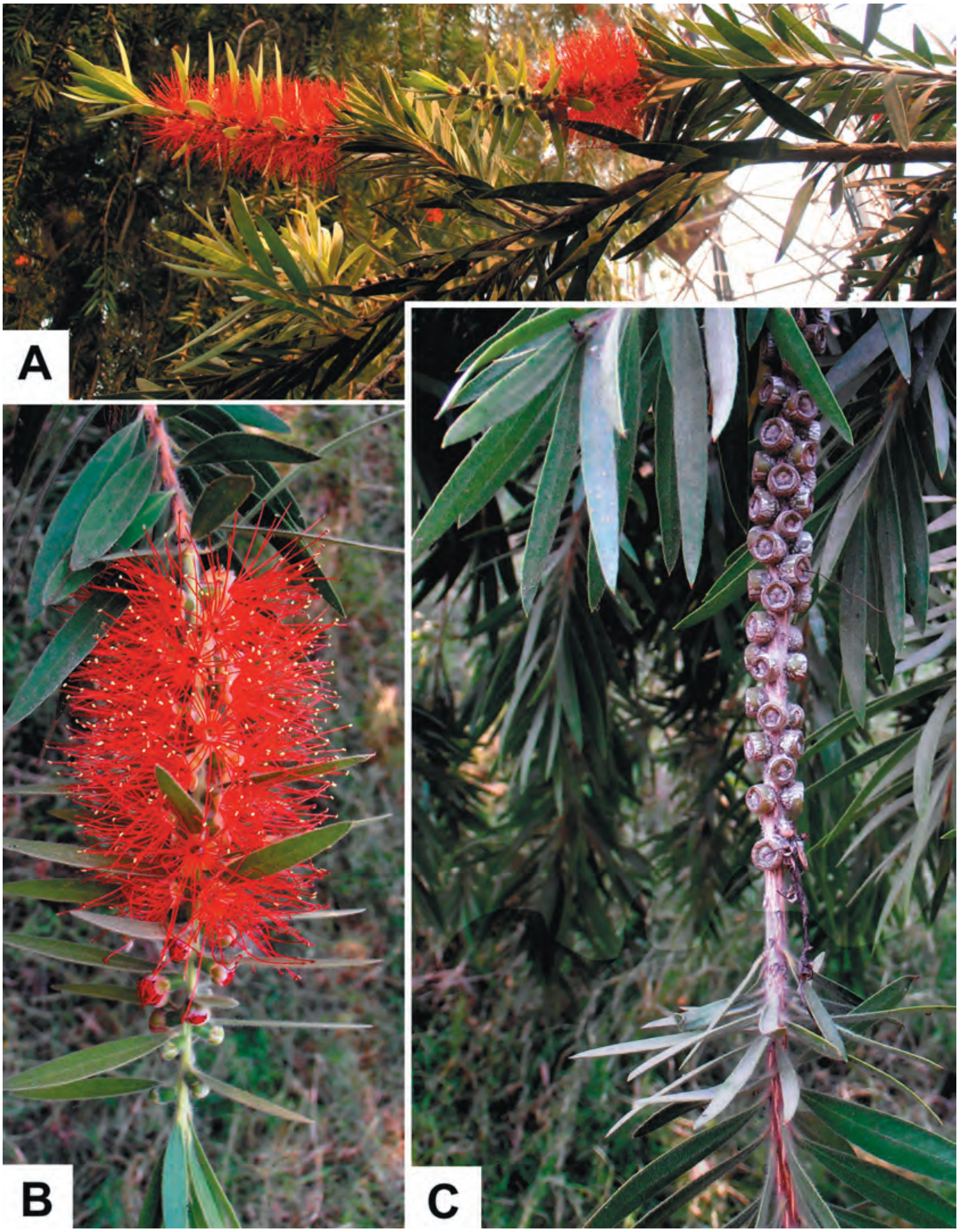

Figure 8. The recent tropical angiosperm *Callistemon linearifolius* (Link) DC, a possible morphological and ecological analogue of *Quasistrobus ramiflorus* Vladimirovich, emend. nov. Photographs are taken from the living plants in Lucknow Botanical Garden, India, by the present author in 2011.

In my opinion, all features, which are characteristic of the classic representatives of Angaropeltaceae, were completely formed and combined in the Early Permian (Kungurian) genera *Sylvocarpus* and *Permoxylocarpus*; then the angaropeltian evolutionary lineage in Wordian (Kazanian) time produced the genera *Angaropeltum* Doweld and *Quasistrobus* Vladimirovich, emend. nov.

Furthermore, in Late Permian, some other angaropeltians appeared (Gomankov & Meyen 1986). This clade continued in Triassic time and finely resulted in the appearance of the order Caytoniales and their close relatives (Petriellales and Corystospermales, but the latter order most probably branched from angaropeltians already in Permian: Zalessky 1934: 253, Fig. 23: *Dicroidium adzvaeanum* Zalessky; see also: Dedeev 1990), e.g. the gymnosperms, which could be regarded as direct predecessors of the angiosperms (Thomas 1938; Anderson & Anderson 1997, 2003; Taylor & Taylor 2009; Bomfleur et al. 2011; opposite viewpoint see in: Hirmer 1937).

Entomophily of the angaropeltian pteridosperms

Discussing morphology of the gymnosperms belonging to the order Peltaspermales, it should be noted that some plants of this order (e.g. *Quasistrobus ramiflorus* or *Peltaspermum morovii* Naug. and some closely related forms) had lobe-like outgrowths or extenuative appendages on the margins of the seed capsules (*Quasistrobus ramiflorus*) or seed-bearing 'megasporangiate' discs (*Peltaspermum morovii*, etc.). Most probably, these outgrowths were orientated outwards only after dissemination of the seeds from the seed-bearing organs. Before that, the outgrowths should be turned downwards and cover the seeds disposed inside the seed-bearing capsules or discs. According to my viewpoint, it is obvious that these outgrows functionally should play a protective role for defense of the ovules/seeds until maturity.

But such a protection would make the pollination process more complicated, if pollination was wind-controlled, because the seeds were covered (completely or partly) by the marginal outgrowths. In that case, the only effective way for pollination of these plants was entomophily.

There are a number of Permian insects with stilets (Palaeodictyoptera; see for further discussion: Sharov 1973) or long trunk-like proboscid mandibles (Homoptera, Hemipsacoptera, Hemiptera; for discussion see: Zalessky 1939). These insects could be orientated trophically to feeding on the seed/ovule content enriched by proteins and carbohydrates. According to my point of view, these insects can be regarded as potential pollinators of the angaropeltians and related plants. Indirectly, this assumption can be supported by the presence of secretory glands on some female reproductive organs of Permian Peltaspermales (discussion see in: Naugolnykh 2018), which could attract potential insect pollinators.

The appearance of a complex evolutionary system with positive 'feed-back' links between all its components causes a situation in which any new adaptation or adaptative trend become more effective or even predictable (Ponomarenko 1996). In these terms, entomophily of some peltaspermalean pteridosperms and, especially, Angaropeltaceae (Naugolnykh & Oskolski 2010) can be regarded as a part of initial phases of angiospermisation as it is understood by Ponomarenko (1996). Thus, the entomophily of peltasperms in wide sense created conditions, in which the initial plant population could be less dense or overpopulated, but at the same time more rich taxonomically, what fits the angiospermisation concept developed by A.G. Ponomarenko.

It is very difficult to look for modern ecological analogues of the angaropeltians in general and *Quasistrobus ramiflorus* in particular, first of all because the recent gymnosperms belong to completely different groups regarding their morphological archetypes. But there are some similar plants among the angiosperms, e.g. *Callistemon linearifolius* (Link) DC (Fig. 8), which is typical of low-latitude tropical and subtropical vegetation and characteristic of the zones with

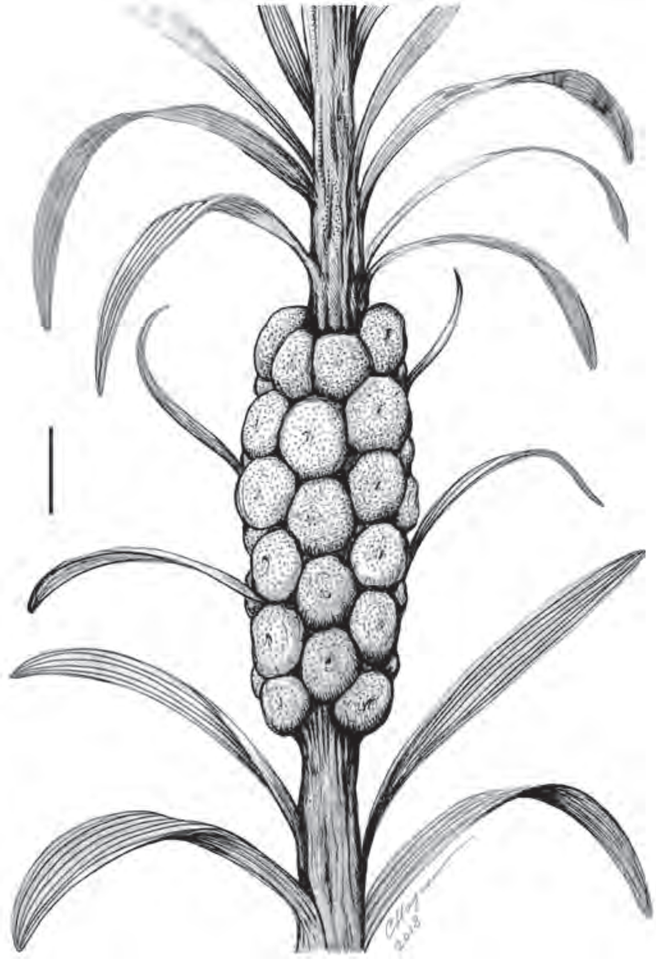

Figure 9. *Quasistrobus ramiflorus* Vladimirovich, emend. nov. Reconstruction of the fertile shoot. Scale bar = 1 cm.

dry summer season. Most probably, macromorphologically the habit of *Quasistrobus ramiflorus*, as it can be reconstructed (Fig. 9) on the basis of the data discussed in this paper, was somewhat similar to *Callistemon linearifolius*, which can also be regarded as potential ecological analogue of *Quasistrobus ramiflorus*.

Acknowledgements

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Address of the author:

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

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Autor(en)/Author(s): Naugolnykh Serge V.

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