Wulfenia **25** (2018): 217–230

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

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

Serge V. Naugolnykh

Summary: The paper is devoted to the monotypic genus *Kuvakospermum* Naug. et Sidorov, emend. nov., which is interpreted as a highly advanced representative of peltasperms (order Peltaspermales). The collection studied includes six specimens of *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov. (four of them are practically completely preserved megasporophylls and two specimens with the seeds preserved in natural connection to reproductive organ, but with the partly or completely detached megasporophyll shield). The megasporophyll is stalked, peltate, with round to ovoid megasporophyll shield with the lobed margin bearing long linear extenuations. Adaxial surface of the megasporophyll shield bears well-developed protective belt. The seeds were attached to adaxial surface of the megasporophyll in the space between the protective belt and the stalk, disposed concentrically around the stalk. Adaxial surface of the megasporophyll bears small secretory glands forming regular parastichies. Abaxial surface of the megasporophyll shield bears numerous small round resin bodies. Some possible fossil relatives and recent morphofunctional analogues of *Kuvakospermum pedatum* are discussed.

Keywords: peltasperms, megasporophylls, Permian, evolution, Angaraland, *Kuvakospermum*

Many new efforts focused on the peltasperm morphology and systematics were published over the past years (Retallack 2002; DiMichele et al. 2005; Galtier & Broutin 2008; Naugolnykh 2008, 2012, Booi et al. 2009; Chaney et al. 2009; Karasev 2009; Mamay et al. 2009; Bomfleur et al. 2011; Zhang et al. 2012). These works were devoted to descriptions of new taxa, which threw new light on the diversity and evolution of this highly sophisticated gymnosperm group. It was clearly proved that the peltasperms originated in Late Carboniferous (Kerp et al. 2001; Naugolnykh 2001b) and reached their highest diversity and real flourishing in the Permian period, when this group was represented by at least three families, i.e. Peltaspermaceae (Thomas) Pilg. et Melchior, Angaropeltaceae Doweld emend. Naugolnykh and Vetlugospermaceae Naugolnykh.

Latest peltasperms existed up to the end of Latest Triassic or perhaps even Jurassic. Most probably, peltasperms s.l. gave rise to the order Caytoniales, which is often regarded as a possible evolutionary source of angiosperm origin (historical review of the problem see in: Thomas 1938; Taylor & Archangelsky 1985; Taylor & Taylor 2009).

The Russian platform, the Cis-Urals and surrounding areas are the regions, where the peltasperms were especially abundant during both the Permian and Triassic (Dobruskina 1975; Gomankov & Meyen 1986; Naugolnykh 2001a, 2012, 2014; Naugolnykh & Sidorov 2012). The most ancient and well-documented find of the seed-bearing disc of the genus *Peltaspermum* Harris (*Peltaspermum goniacanthus* Naugolnykh), was also discovered here, in the Upper Carboniferous deposits of the Southern Urals (Naugolnykh 2001b), in the famous Aidaralash locality. Exact

age of this find was proved by stratigraphic data based on conodonts, fusulinids and ammonoid fauna (Davydov et al. 1998). Thus, significance of that region for deeper understanding of the peltasperm evolution and systematics is obvious.

The present paper deals with the peltasperm *Kuvakospermum pedatum* Naugolnykh et Sidorov, 2012, emend. nov., which is reconsidered on the basis of the new finds, allowing the proposal of a newly emended diagnosis of the genus *Kuvakospermum* Naugolnykh et Sidorov, 2012 and the revision of the morphological concept of this uncommon and distinct peltaspermalean plant.

Materials and methods

All the specimens studied came from the Novy Kuvak locality, in Shentalinsk District of the Samara region, Russia, nearby the village Novy Kuvak. The locality is a quarry, where sandstones and marbles crop out. Stratigraphically, the locality belongs to the Kazanian stage of the Middle Permian (former Upper Permian according to the traditional stratigraphical nomenclature) and can be considered as Wordian according to the International Stratigraphical scale and charts.

Floristic assemblage of the Novy Kuvak locality includes equisetophytes *Paracalamites* spp., diverse peltasperms represented by both reproductive organs (*Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov., *Peltaspermum qualenii* Naugolnykh, *P. morovii* Naugolnykh) and sterile leaves (*Permocallipteris wangenheimii* (Fischer) Naugolnykh, *Permocallipteris* spp.; *Compsopteris salicifolius* (Fischer) Naugolnykh, *Comia* sp.); ginkgophytes (female reproductive organs *Karkenia* sp., leaves *Psygmophyllum* spp., *Kerpia belebeica* Naugolnykh and some other taxa which have not been properly studied yet), male reproductive organs of peltasperm or ginkgophyte affinity *Permotheca colovratica* Naugolnykh; vojnovskyaleans (female reproductive organs *Suchoviela* sp., leaves *Rufloria* sp., seeds *Megasylvella* cf. *ivagorica* Naugolnykh).

The plant remains are mostly represented by limonitizied compressions and impressions. Cuticles resistant enough for maceration have not been found.

The collection studied is kept at the Geological-Mineralogical Museum of the Samara State Technical University, the City of Samara (spec. 1317 [holotype]; P0061; P0062; P0430; P0444, and supplementary specimens), and at the Geological Institute of Russian Academy of Sciences, GIN RAS, Moscow (spec. 4851/338).

Paleobotanical description

Class Peltaspermopsida Cronquist, 1981

Order Peltaspermales Taylor, 1981

Family Peltaspermaceae Thomas, 1933

Kuvakospermum Naugolnykh et Sidorov, 2012, emend. nov.

Type species. *Kuvakospermum pedatum* Naugolnykh et Sidorov, Kazanian stage (Middle Permian), the European part of Russia.

Emended diagnosis. Megasporophyll stalked, peltate, with round to ovoid megasporophyll shield with lobed margins bearing long linear extenuations. Adaxial surface of megasporophyll shield with well-developed protective belt. Seeds attached to adaxial surface of megasporophyll in space

between protective belt and stalk. Seeds arranged concentrically around stalk. Adaxial surface of megasporophyll with small secretory glands forming regular parastichies. Abaxial surface of megasporophyll shield covered by numerous small round to ovoid resin bodies.

Kuvakospermum pedatum Naugolnykh et Sidorov, 2012, emend. nov. (Figs 1A–D; 2A–C; 3A–C; 4A–D; 5A–C; 6A–B; 7A–B)

Selected synonymy

Noeggerathiophyte indet. (Naugolnykh & Sidorov 2011: 65–66, Plate I, Figs 1–2; Text-fig. 1)

Kuvakospermum pedatum Naugolnykh et Sidorov (Naugolnykh & Sidorov 2012: 72–73, Plate I, Figs 1–4, Text-fig. 1)

Holotype. Spec. 1317; Geological-Mineralogical Museum of the Samara State Technical University, the City of Samara, Russia, locality Novy Kuvak, Kazanian (Wordian), Middle Permian; figured here on Fig. 1A, B.

Emended diagnosis. Same as that of the genus.

Description. The collection studied includes six specimens attributed to this species. Three of them are almost completely preserved stalked, seed-bearing megasporophylls (Figs 1A, B, D; 2C; 3A–C; 4A, C, D; 5C), two others are fragmentarily preserved megasporophylls with detached shields but with the well-preserved imprints of radially arranged seeds (strictly saying, ovules) and partly preserved stalk, presumably belonging to not adult seed-bearing organs (Figs 1C; 5A, B). The initial material which was used as a basis for the description of the species was only a holotype (numbered 1317); but the counterpart of the holotype was found after additional collecting (Fig. 2A–C). One more specimen was initially misunderstood as a possible reproductive organ of noeggerathiophyte affinity (Naugolnykh & Sidorov 2011; see here Fig. 1D), but newly collected material allowed to make more correct identification of this specimen as the flattened upper part of the megasporophyll shield.

The megasporophyll is peltate and consists of a central stalk distally attached to the central part of the round or ovoid megasporophyll shield. Margins of the shield bear long linear lobes with acute tips. Adaxial surface of the megasporophyll shield possesses a protective belt disposed around the central stalk. The seeds are situated inside the space between stalk and protective belt. Arrangement of the seeds is radial, around the central stalk. Number of seeds varies from ten to eleven, judging from the most informative specimens with the preserved seeds (Fig. 5A, B; only one half of the megasporophyll with five seeds is seen in Fig. 5A; therefore complete number of the seeds should be ten to eleven, as it can be seen on the specimen figured in Fig. 5B). One specimen shows the seeds preserved in natural connection to the adaxial surface of the megasporophyll shield (Fig. 5C).

The protective belt is covered by fine prolonged folds and striation (Figs 1A, B; 2C; 7B). Width of the protective belt is about 15–20 mm and, thus, it exceeds length of the seeds, which is about 10 mm. It can be easily explained as a result of protecting and covering the seeds by the protective belt when the seeds (i.e. ovules) were not adult. Seeds of long-ovoid shape (Fig. 5A), with the maximal width at the seed base (in halazal area). Maximal observed width of the seed is 5 mm.

Central stalk of the megasporophyll is cylindrical, with smooth surface (Figs 1A, B; 2C; 3B), width of the stalk is about 1 cm; length is about 8 cm. Upper part of the stalk can be slightly

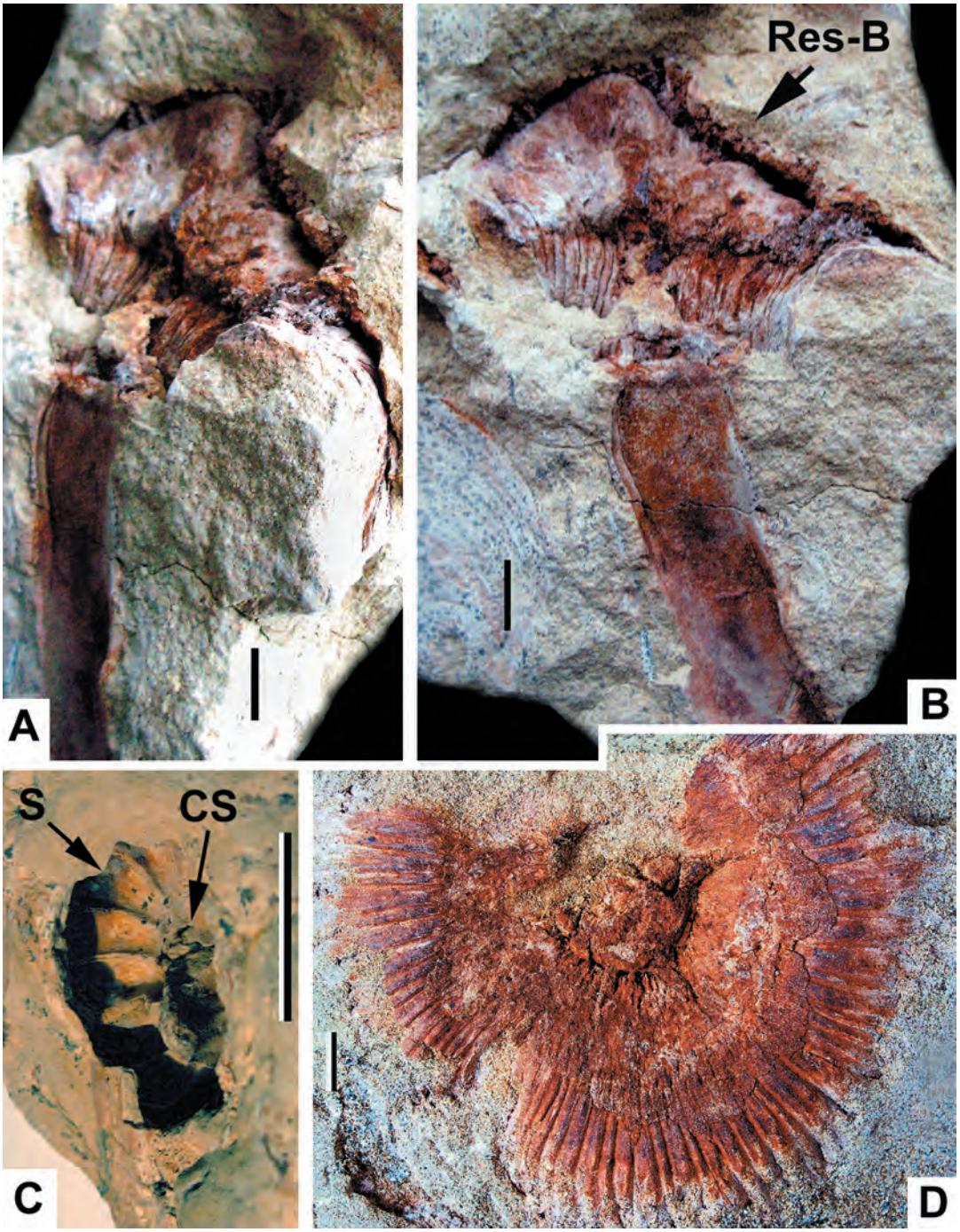

Figure 1. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov. A, B – holotype 1317, Res-B – resin bodies; C – spec. P0444, S – seeds preserved as imprints, CS – central stalk; D – morphology of the megasporophyll shield with linear marginal lobes, reproduced from: Naugolnykh, Sidorov, 2011, Plate I, fig. 1. Locality: Novy Kuvak. Scale bars = 1 cm.

narrower than the middle and basal parts. There is small concentric ring-like structure around the stalk, which corresponds to the place where the protective belt was attached to the stalk before seeds become adult.

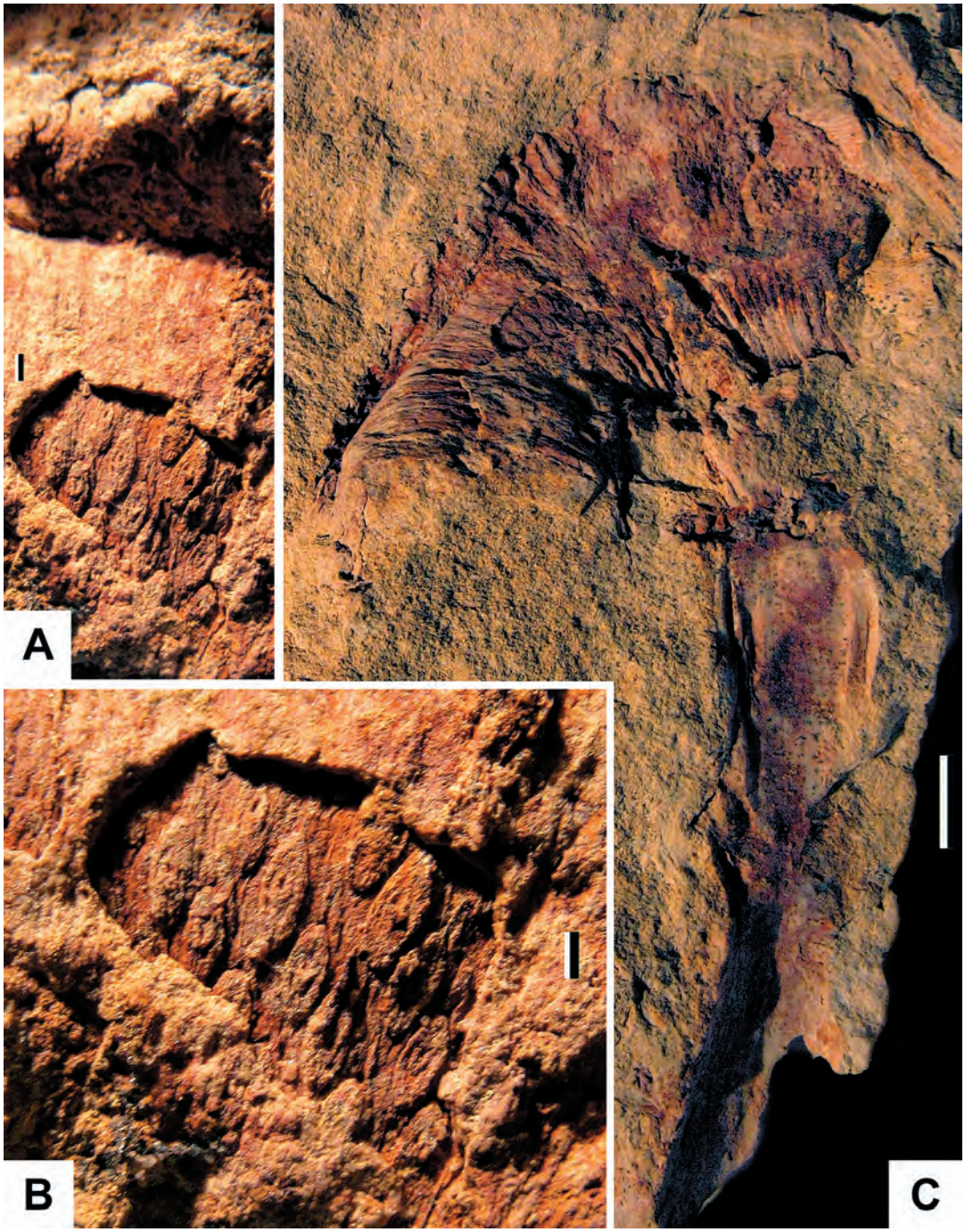

Figure 2. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov.; counterpart of the holotype. A – secretory glands on the adaxial surface of the megasporophyll; B – general morphology of the stalked megasporophyll; C – detailed view on the secretory glands; A–C – spec. P0430. Locality: Novy Kuvak. Scale bars = 1 cm (C); 1 mm (A, B).

Central part of the megasporophyll shield was relatively thick (Figs 1A, B; 2C; 7A, B) and most probably more or less fleshy when the plant was alive. Maximal thickness is disposed at the megasporophyll center and is about 2 cm. Diameter of the megasporophyll shield (including marginal lobe-like extenuations) is up to 12 cm. Upper (abaxial) surface of the megasporophyll

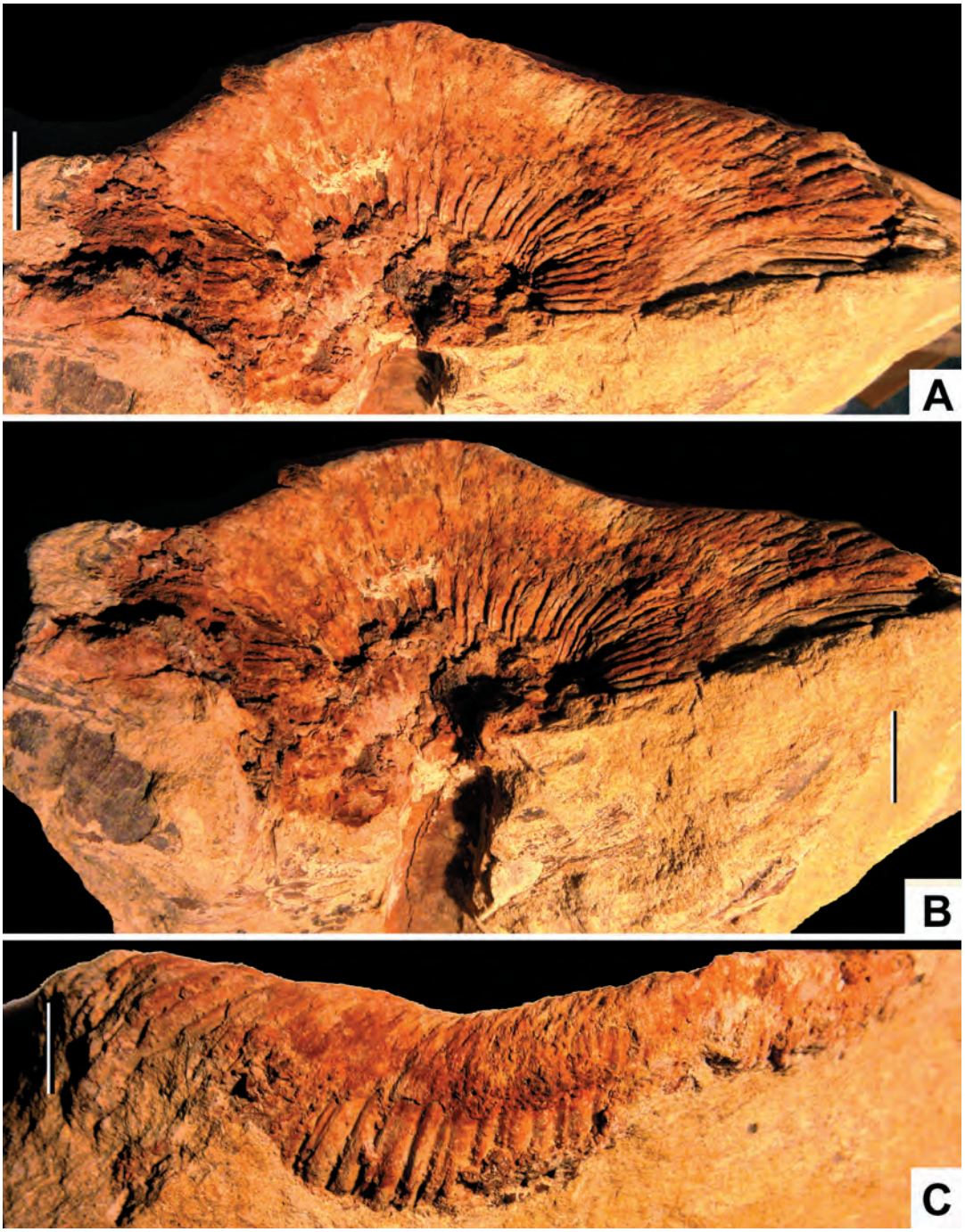

Figure 3. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov. A – megasporophyll shield, upper side view; B – megasporophyll shield and a stalk, lateral view; C – lobed margin of the megasporophyll; A–C – spec. P0062. Locality: Novy Kuvak. Scale bars = 1 cm.

shield was densely covered by small round or ovoid bodies (Figs 1B; 4B; 6B; 7A, B), which are interpreted here as resin bodies typical of the most peltasperms. Practically, the identical resin bodies, but loosely arranged, are described for the radially symmetrical megasporophylls of peltasperms from the Lower Permian locality Bou Achouch, Morocco (Kerp et al. 2001, Figs 3,

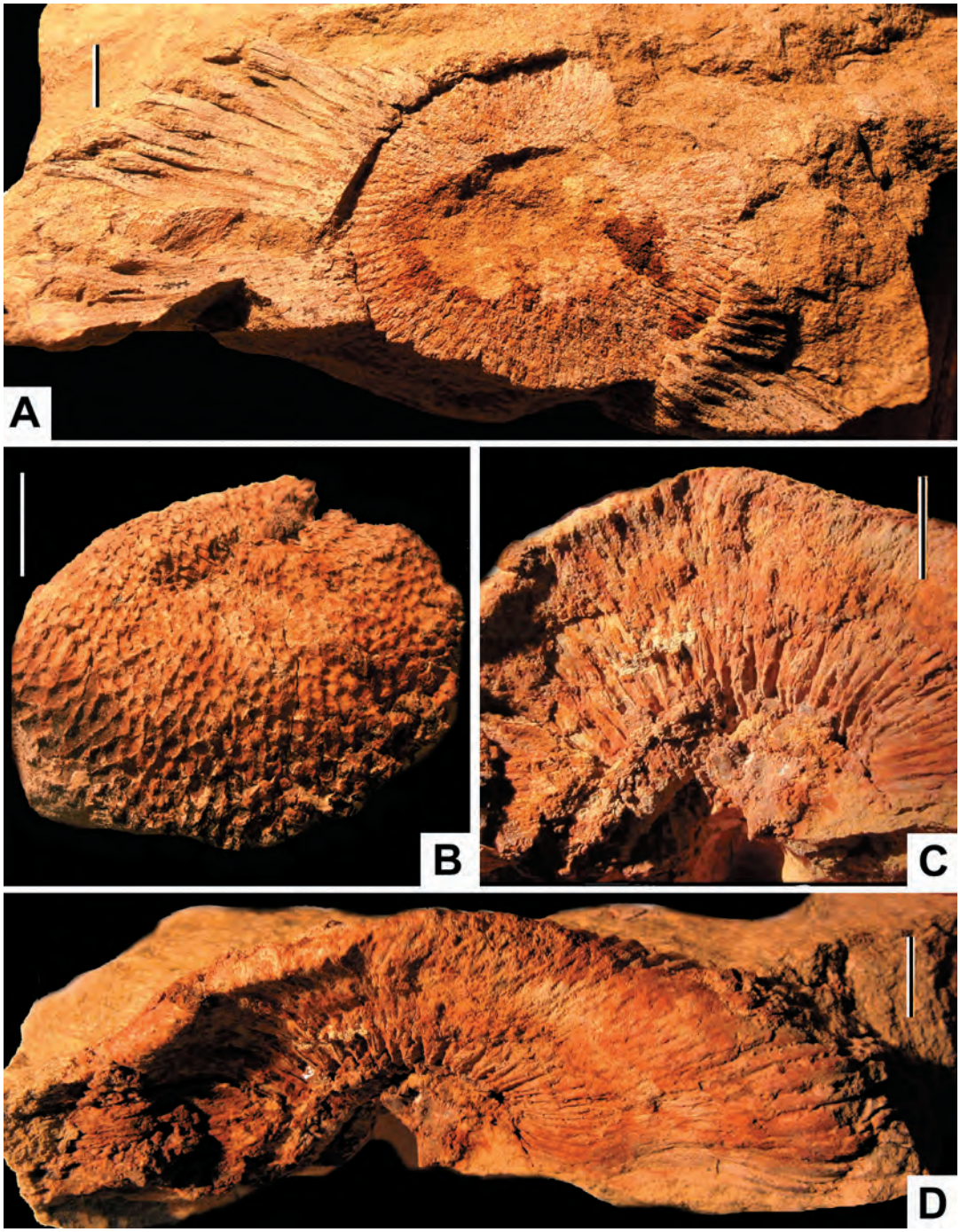

Figure 4. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov. A – spec. P0061, adaxial surface of the megasporophyll, stalk is detached; B – spec. P0062a, supplementary specimen showing upper (abaxial) surface of the central part of the megasporophyll covered by numerous resin bodies; C, D – spec. P0062; adaxial surface of the megasporophyll shown in different side light. Locality: Novy Kuvak. Scale bars = 1 cm.

4, 5), and figured for the seed-bearing megasporophylls of the vetlugospermacean peltasperm *Navipelta resinifera* Karasev (Karasev 2009, Plate 20, Figs 2, 3). These resin bodies most probably had protective function against the herbivorous insects or other arthropods.

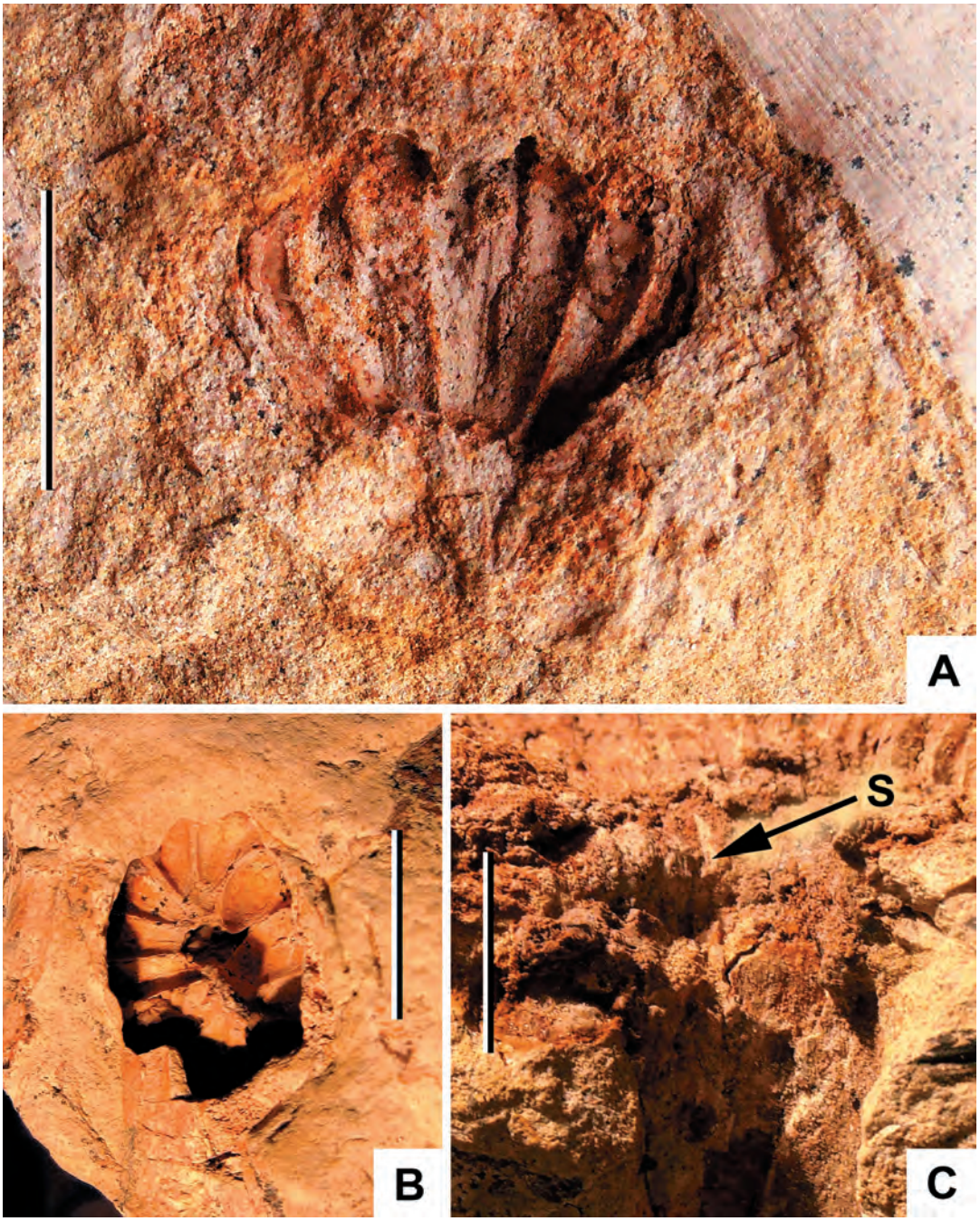

Figure 5. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov. A – spec. 4851/338, specimen with the seeds arranged around the central stalk, the megasporophyll shield is partly detached; B – spec. P0444, imprints of the seeds preserved in natural position around the central stalk; C – spec. P0062, central part of the stalked megasporophyll, S – seeds in attachment. Locality: Novy Kuvak. Scale bars = 1 cm.

A very uncommon feature of *Kuvakospermum pedatum* is the presence of regularly arranged structures of ovoid to rhombic shape disposed on the lower (adaxial) surface of the megasporophyll shield between the lobed shield margin and the protective belt (Figs 2A–C; 4A; 7A). These structures are interpreted here as secretory glands, which probably secreted/released special

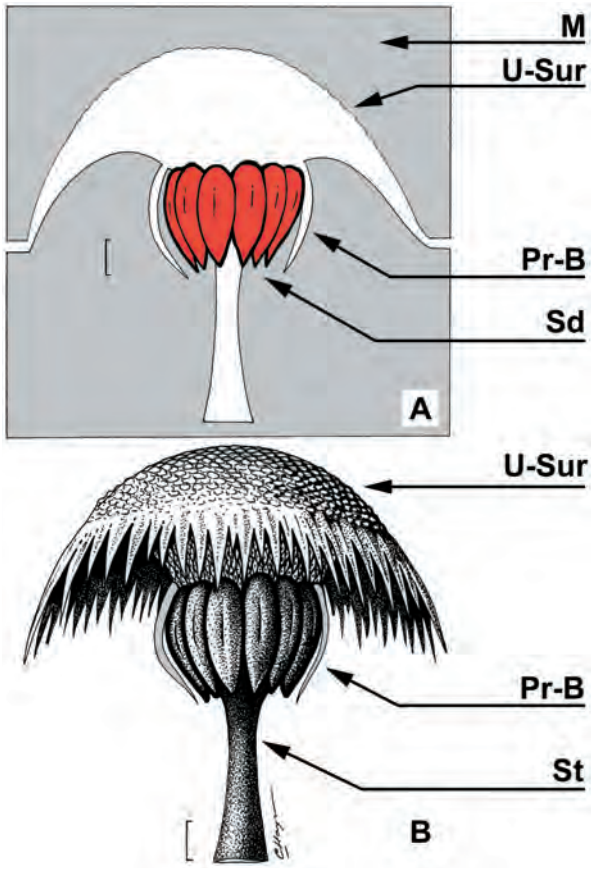

Figure 6. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov. Type and modes of preservation (A) and general scheme of morphological structure (B). Abbreviations: M – matrix; U-Sur – upper (abaxial) surface of megasporophyll; Pr-B – protective belt; Sd – seeds in attachment; St – megasporophyll stalk. Scale bars = 1 cm.

substances to attract insects for pollination (for details see 'Discussion' below). The glands have rhomboid shape with one well-pronounced concentric fold and a small pit at the center (Fig. 2B). The glands form regular parastichies on the adaxial surface of the megasporophyll shield.

Exact sterile leaves of *Kuvakospermum pedatum* are still unknown, but there is an indirect evidence that they could be of callipterid morphology. Several callipterid species are known in the Novy Kuvak locality, i.e. *Permocallipteris wangenheimii* (Fischer) Naugolnykh, *Compsopteris salicifolius* (Fischer) Naugolnykh and *Comia* sp. The leaves of *Permocallipteris wangenheimii* are associatively linked with the female reproductive organs of *Peltaspermum qualenii* Naugolnykh, what is proved by repeating co-occurrence of them in a number of localities of Kazanian stage of the Russian platform and Cis-Urals. Thus, it is possible that *Kuvakospermum pedatum* with female reproductive organs had leaves like *Compsopteris salicifolius* (Fischer) Naugolnykh, as it was suggested in the protologue (Naugolnykh & Sidorov 2012) or like *Comia* sp. The leaves of *Compsopteris*-like morphology are broadly distributed in Permian deposits around the world (Halle 1927; Sze 1955; Chow et al. 1955; Mamay & Breed 1970; Gand et al. 1997; Wang 1997). Leaves of that type are often associated with the peltasperm female reproductive organs.

Material. Six megasporophylls including four practically complete specimens and two specimens with seeds, but with a partly or completely detached megasporophyll shield.

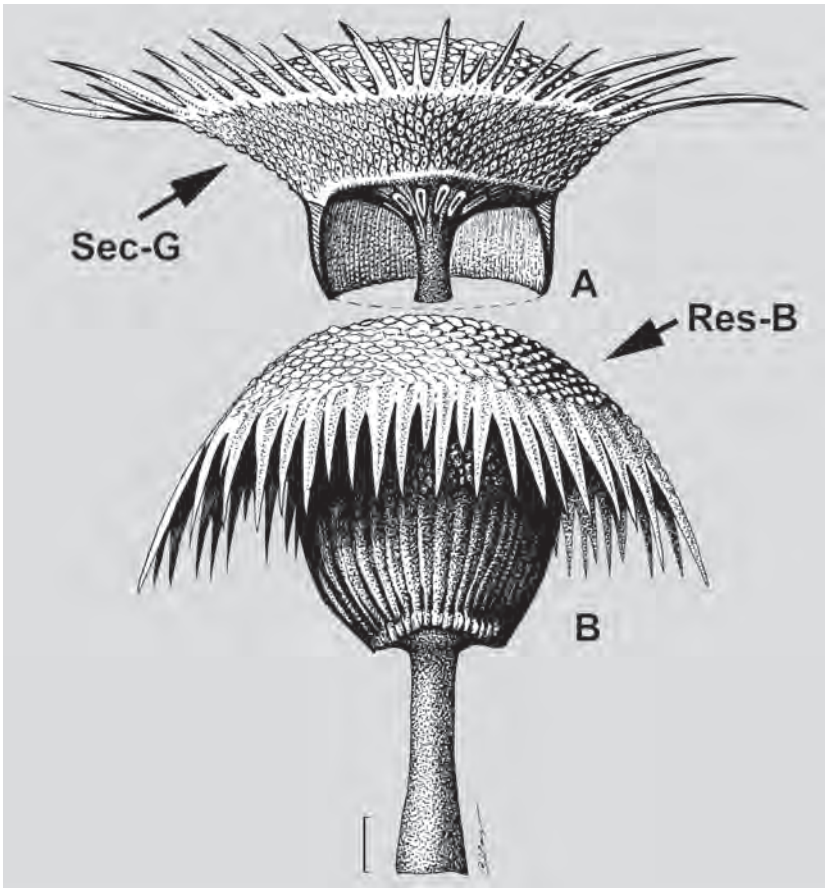

Figure 7. *Kuvakospermum pedatum* Naugolnykh et Sidorov, emend. nov., reconstruction of the peltate megasporophyll. A – marginal lobes (extenuations) curved upwards; B – marginal lobes (extenuations) curved downwards; Sec-G– secretory organs (glands); Res-B – resin bodies. Scale bar = 1 cm.

Discussion

The first feature which distinguishes *Kuvakospermum pedatum* from other peltasperm megasporophylls is its extremely large size. Most of the megasporophyll shields of peltasperms are about 1 cm in diameter or less, sometimes somewhat larger, up to 2.5 cm in diameter, for instance the megasporophylls of *Peltaspermum petaloides* Naugolnykh from the Kungurian (Lower Permian) deposits of the Cis-Urals (Naugolnykh 2016). Gigantic size of the megasporophylls of *Kuvakospermum pedatum* can be explained by polyploidization, which often takes place in island vegetation. Large size of other gymnosperm organs, which is typical of plants of the locality Novy Kuvak, can be explained by the same reason, which indirectly points to the possible island origin of the Novy Kuvak locality. This island could be placed in the Kazanian sea, which occupied a large part of the eastern segment of the Russian platform in that time.

The protective belt of *Kuvakospermum pedatum* is homologous to the protective ridge of *Vetlugospermum* Naugolnykh (Naugolnykh 2012, Fig. 7). Presence of this structure could be a reason for possible assignment of the genus *Kuvakospermum* to the family Vetlugospermaceae, but megasporophylls of true Vetlugospermaceae (*Vetlugospermum, Navipelta* Karasev) are always clearly bilaterally symmetrical in contrast to radially symmetrical megasporophylls of

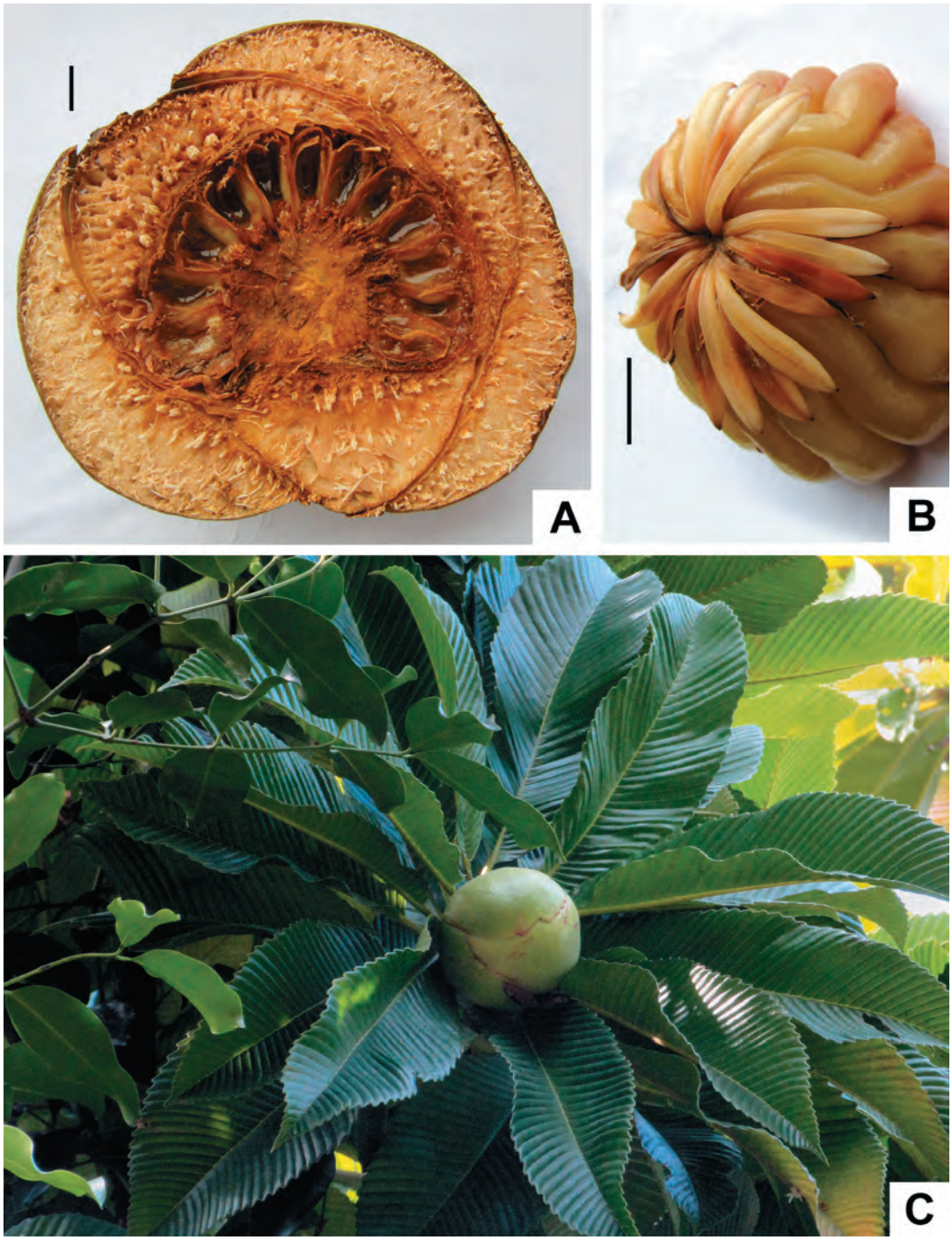

Figure 8. *Dillenia indica* L., Campus of the Sun Yat-sen University, 'Bamboo Garden', the City of Guangzhou, Guangdong Province, China. Scale bars = 1 cm (A, B); C – without scale.

Kuvakospermum. Because of that, the genus *Kuvakospermum* is provisionally and conditionally assigned to the family Peltaspermaceae. Taxonomical position of *Kuvakospermum* inside the order Peltaspermales assumed as well-based regarding both general morphology of the peltate stalked megasporophylls and position and arrangement of the seeds.

The putative secretory glands of *Kuvakospermum pedatum* are of particular interest, because such features are more typical of angiosperms rather than gymnosperms, although similar glands were reported for some Late Palaeozoic pteridosperms s.l. (Kellogg et al. 2002; Krings et al. 2002), and even for the peltasperms s.str. (Naugolnykh & Kerp 1996, Plate V, Figs 9, 10).

Similar concentrically organized glands are known for the recent angiosperms of the family Plumbaginaceae (Grigore & Toma 2016). Normally, secretory glands are much smaller, but somewhat larger multicellular glands and extrafloral nectaries are also known (Diaz-Castelazo et al. 2005), and some of them have similar shape (Diaz-Castelazo et al. 2005; Figs 2E, 3B, 4B; Machado et al. 2008; Sawidis 2012, Fig. 5) and can be arranged in a similar dense pattern (Diaz-Castelazo et al. 2005, Fig. 2F) although they are still quite small. The glands ('protonectaries') of *Kuvakospermum pedatum* could serve as secretory sources of the pheromones for attracting insects involved in pollination process as it was suggested for the other peltasperm (angaropelt) species *Permoxylocarpus trojanus* Naugolnykh (Naugolnykh & Oskolski 2010).

Morphofunctionally (but not anatomically in full sense), the seed-bearing megasporophylls of *Kuvakospermum pedatum* have many features in common with several present-day angiosperms, for example, tropic *Dillenia indica* L. also known as 'elephant apple' (Fig. 8). Fruits of *D. indica* also have radially arranged seeds disposed around the central stalk-like structure and they are covered by fleshy protective sepals, functioning like the protective belt of *Kuvakospermum pedatum*.

Acknowledgements

This work was funded by the subsidy of the Russian Government to support the Program of Competitive Growth of Kazan Federal University among World's Leading Academic Centers. The work was fulfilled in a framework of the State program 0135-2016-0001 of the Geological Institute of RAS and was supported by the RFBR project 18-04-00322. The author expresses his sincere gratitude to A.A. Sidorov (Geological-Mineralogical Museum of the Samara State Technical University, the City of Samara), who provided his collection for the present study.

References

Bomfleur B., Taylor E. L., Taylor T. N., Serbet R., Krings M. & Kerp H (2011): Systematics and paleoecology of a new peltaspermalean seed fern from the Triassic polar vegetation of Gondwana. – Int. J. Pl. Sci. **172**(6): 807–835.

Booi M., van Waveren I. M. & van Konijnenburg-van Cittert J. H. A. (2009): *Comia* and *Rhachiphyllum* from the early Permian of Sumatra, Indonesia. – Rev. Palaeobot. Palynol. **156**: 418–435.

Chaney D. S., Mamay S. H., DiMichele W. A. & Kerp H. (2009): *Auritifolia* gen. nov., probable seed plant foliage with comioid affinities from the Early Permian of Texas, USA. – Int. J. Pl. Sci. **170**(2): 247–266.

Chow T. Y., Chang S. I. & Chang L. C. (1955): An additional specimen of forked frond of *Protoblechnum wongii* Halle. – Acta Palaeontol. Sin. **3**(3): 167–171.

Davydov V. I., Glenister B. F., Spinosa C., Ritter S. M., Chernykh V. V., Wardlaw B. R. & Snyder W. S. (1998): Proposal of Aidaralash as Global Stratotype Section and Point (GSSP) for the base of the Permian system. – Episodes **21**(1): 11–18.

Diaz-Castelazo C., Rico-Gray V., Ortega F. & Angeles G. (2005): Morphological and secretory characterization of extrafloral nectaries in plants of coastal Veracruz, Mexico. – Ann. Bot. **96**: 1175–1189.

DiMichele W.A., Kerp H., Krings M. & Chaney D.S. (2005): The Permian peltasperm radiation: evidence from the Southwestern United States. The Nonmarine Permian. – New Mexico Mus. Nat. Hist. Sci. Bull. **30**: 226–242.

Dobruskina I.A. (1975): A role of the peltaspermalean pteridosperms in Permian and Triassic floras. – Paleontol. J. **4**: 120–132.

Galtier J. & Broutin J. (2008): Floras from red beds of the Permian Basin of Lodève (Southern France). – J. Iberian Geol. **34**(1): 57–72.

Gand G., Kerp H., Parsons C. & Martinez-Gareia E. (1997): Palaeoenvironmental and stratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Pena Sagra, Cantabrian Mountains, Spain). – Geobios **30**(2): 295–318.

Gomankov A.V. & Meyen S.V. (1986): Tatarina flora. Composition and distribution in the Late Permian of Eurasia. – Trudy Geol. Inst. Akad. Nauk S.S.S.R. **401**. [In Russian]

Grigore M.N. & Toma M.N. (2016): Structure of salt glands of Plumbaginaceae. Rediscovering old findings of the 19th century: 'Mettenius' or 'Licopoli' organs? – J. Plant Develop. **23**: 37–52.

Halle T.G. (1927): Palaeozoic plants from Central Shansi. – Palaeontol. Sin., Ser. A **2**(1): 5–316.

Karasev E.V. (2009): A new genus *Navipelta* (Peltaspermales, Pteridospermae) from the Permian/Triassic Boundary Deposits of the Moscow Syneclise. – Paleontol. J. **43**: 1262–1271.

Kellogg D.W., Taylor T.N. & Krings M. (2002): Effectiveness in defense against phytophagous arthropods of the cassabanana (*Sicana odorifera*) glandular trichomes. – Entomol. Exp. Appl. **103**: 187–189.

Kerp H., Broutin J., Lausberg S. & Aassoumi H. (2001): Discovery of latest Carboniferous – early Permian radially symmetrical peltaspermaceous megasporophylls from Europe and North Africa. – Compt. Rend. Acad. Sci. Paris, Sér. IIa **332**(8): 513–519.

Krings M., Taylor T.N. & Kellogg D.W. (2002): Touch-sensitive glandular trichomes: a mode of defence against herbivorous arthropods in the Carboniferous. – Evol. Ecol. Res. **4**: 779–786.

Machado S.R., Morellato L.R.C., Sajo M.G. & Oliveira P.S. (2008): Morphological patterns of extrafloral nectaries in woody plant species of the Brazilian cerrado. – Pl. Biol. **10**: 660–673.

Mamay S.H. & Breed W.J. (1970): Early Permian plants from the Cutler Formation in Monument Valley, Utah. – Geological Survey Research. US Geological Survey Professional paper. **700** B: 109–117.

Mamay S.H., Chaney D.S. & DiMichele W.A. (2009): *Comia*, a seed plant possibly of peltaspermous affinity: a brief review of the genus and description of two new species from the Early Permian (Artinskian) of Texas, *C. greggii* sp. nov. and *C. craddockii* sp. nov. – Int. J. Pl. Sci. **170**(2): 267–282.

Naugolnykh S.V. (2001a): A new peltaspermaceous pteridosperm from the Upper Permian of the Russian platform – Palaeobotanist **50**: 189–205.

Naugolnykh S.V. (2001b): Paleobotany of the Upper Carboniferous/Lower Permian of the Southern Urals. Part 3. Generative organs of gymnosperms. – Permophiles **39**: 19–23.

Naugolnykh S.V. (2008): A new gymnosperm *Sylvocarpus armatus* gen. et sp. nov. from the Lower Permian of the Ural Mountains. – Paleontol. J. **42**: 431–439.

Naugolnykh S.V. (2012): *Vetlugospermum* and Vetlugospermaceae: a new genus and family of peltasperms from the Lower Triassic of Moscow syneclise (Russia). – Geobios **45**: 451–462.

Naugolnykh S.V. (2014): *Permocallipteris*, a new genus from the Permian of Angaraland. – Wulfenia **21**: 1–20.

Naugolnykh S.V. (2016): Flora Permica. Plant world of Permian period, Cis–Urals. – Trudy Geol. Inst. **612**: 1–336. [In Russian]

Naugolnykh S.V. & Kerp H. (1996): Aspects of Permian Palaeobotany and Palynology. XV. On the oldest known peltasperms with radially symmetrical ovuliferous discs from the Kungurian (uppermost Lower Permian) of the Fore-Urals (Russia). – Rev. Palaeobot. Palynol. **91**: 35–62.

Naugolnykh S.V. & Oskolski A.A. (2010): An advanced peltasperm *Permoxylocarpus trojanus* Naug. from the Lower Permian of the Urals (Russia): an ancient case of entomophily in gymnosperms? – Wulfenia **17**: 29–43.

Naugolnykh S.V. & Sidorov A.A. (2011): The first find of a reproductive organ of neggerathiophyte in Permian deposits of Russia. – In: Evolution of the organic world in the Paleozoic and Mesozoic in collections and exposition of natural-history museums: 65–69. – St-Petersburg: Mamatov. [In Russian]

Naugolnykh S.V. & Sidorov A.A. (2012): A new representative of gymnosperms of the order Peltaspermales from the Novy Kuvak locality (Kazanian stage, Samara region, Russia). – In: Naugolnykh S.V. [ed.]: Palaeontology and evolution of the biodiversity in the Earth history (in museum context). Collection of scientific articles: 71–78. – Moscow: Geos. [In Russian]

Retallack G.J. (2002): *Lepidopteris callipteroides*, an earliest Triassic seed fern of the Sydney Basin, southeastern Australia. – Alcheringa **26**: 475–500.

Sawidis T. (2012): The secretory glands of *Asphodelus aestivus* flower. – In: Mworia J. [ed.]: Botany: 131–162. – Rijeka: InTech.

Sze H.C. (1955): On a forked frond of *Protoblechnum wongii* Halle. – Acta Palaeontol. Sin. **3**(1): 11–24.

Taylor E.L. & Taylor T.N. (2009): Seed ferns from the late Paleozoic and Mesozoic: any angiosperm ancestors lurking there? – Amer. J. Bot. **96**: 237–251.

Taylor T.N. & Archangelsky S. (1985): The Cretaceous pteridosperms *Ruflorinia* and *Ktalenia* and implications on cupule and carpel evolution. – Amer. J. Bot. **72**(12): 1842–1853.

Thomas H.H. (1938): Pteridosperm evolution and the angiospermae. – Deuxième Congrès pour l'avancement des études de stratigraphie Carbonifère, Heerlen, 1935. – Compte rendu, tome **3**: 1311–1321.

Wang Z.-Q. (1997): Permian *Supaia* fronds and an associated *Autunia* fructification from Shanxi, China. – Palaeontology **40**: 245–277.

Zhang Y., Zheng S. & Naugolnykh S.V. (2012): A new species of *Lepidopteris* discovered from the Upper Permian of China, with its stratigraphic and biologic implications. – Chin. Sci. Bull. **57**(27): 3603–3609.

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