Taimyria gen. nov., a new genus of evolutionary advanced gymnosperms from Triassic of the Taimyr Peninsula, Siberia, Russia

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Abstract: New genus and species Taimyria triassica NAUGOLNYKH et MOGUTCHEVA gen. et sp. nov. of peltaspermalean affinity is described on the basis of material collected from the Keshinskian Formation (Induan stage, Lower Triassic), outcropped in the Tsvetkov Cape section (eastern part of the Taimyr Peninsula, Siberia, Russia). This new plant is characterized by both macro- and microstructural features. Taimyria triassica has long racemose aggregations (cones or megastrobili) consisting of an axis with peltate seed-bearing discs (which also can be interpreted as seed-bearing semi-closed capsules), with margins curved adaxially. The seed-bearing discs are round to ovoid, with short stalk connected at central area of the adaxial part, and attached to the cone axis nearly perpendicularly, in a dense spiral pattern. Six to eight seeds are concentrically displayed around the stalk on the adaxial surface of the discs. The seeds preserved in seed-bearing discs were extracted from macerated reproductive organs and described as well. The seeds are platyspermic, ovoid, narrower at their apical micropylar end orientated toward the disc stipe. Problems of systematics and general evolutionary trends of the order Peltaspermales are briefly discussed.

Key words: gymnosperms, peltasperms, Triassic, Siberia, new taxa, morphology, evolution

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Introduction

The Early Triassic flora of Siberia is very uncommon and interesting for both reconstruction of origin and further evolution of early Mesozoic floras of Northern Eurasia, and even in a context of global florogenetic processes. Nonetheless, for a long time, our knowledge of this flora was far from ideal.

Fossil plants from the Triassic deposits of Siberia are stratigraphically known from the lowermost part of the Triassic system, i.e., since the Induan, in contrast to floras of many other regions of Eurasia, where plant megafossils are found only from the Olenekian stage (Dobruskina 1982), with some very random exceptions (Lozovsky et al. 2001, Naugolnykh 2012, Arefiev et al. 2015).

The Early Triassic (Induan) floras of Siberia have a small number of taxa in common with the early Permian floras-predecessors in this region. The Early Triassic flora of Siberia includes some endemic and quite peculiar plant taxa, for instance, the very particular peltasperm, which is in the scope of the present paper. These taxa have florogenetic links between the Early Triassic flora of Siberia and older late Permian floras of that region, and even with the remote floras of Middle to Late Triassic age, from when similar peltasperms are also known (Stanislavsky 1976, Khramova 1977, Schweitzer and Kirchner 1998, Anderson and Anderson 2003).

The peltasperms sensu lato (representatives of the order Peltaspermales) are of special interest and importance in this context, because these plants link the late Permian and Early Triassic floras of Siberia, and they played an important role in the evolution of vegetation at the Palaeozoic/Mesozoic boundary, showing the morphogenetical transformations that took place in this plant group’s evolution during that time.

The taxonomical position of the peltasperms sensu stricto (the family Peltaspermaeae PILG. et MELOCH., validation of the family) is not absolutely clear and unequivocal, and is still controversial and disputable. Some palaeobotanists consider this family (or even the order Peltaspermales as a whole) as a member of pteridosperms (Taylor and Taylor 1993, Taylor et al. 2009). Some others believe that the peltasperms are ancestral plants for the class Ginkgoopsida (Meyen 1987). This problem closely connects to the definition of phylogenetic relationships between two more
families of the order Peltaspermales, i.e., Angaropeltaceae *Doweld* sensu Naugolnykh (2012) and Vetlugospermaceae *NaugolNykh*. For the discussion of the authors’ concept of peltasperm systematics see Naugolnykh (2008, 2012, 2018, 2019).


The second aspect, which made the situation with the peltasperm systematics and taxonomy even more complicated, reflects the necessity of improving or analyzing only of such taxa for which we do have data on both reproductive organs and leaves. It is very helpful if in situ pollen and seeds of these plants are also known. All the organs should be characterized by both macromorphological and microstructural (such as epidermal) data.

The main part of the present article is devoted to description of a new peltasperm taxon from the Lower Triassic volcanogenic-sedimentary deposits cropped out in the eastern part of the Taimyr Peninsula. Good preservation of the material allowed studying both macromorphology and epidermal-cuticular characters/features of the plant, which is within the scope of the descriptive part of this paper.

The second part of the paper includes briefly summarized main principles of peltasperm systematics, taxonomic content of the families Peltaspermaceae, Angaropeltaceae and Vetlugospermaceae, a content and taxonomic status of the order Peltaspermales, and the place of peltasperms in gymnosperm systematics and evolution.

**Material and methods**

The unique single specimen for the present study originated from the fossil plant locality disposed along the south-eastern coast of the Tsvetkov Cape in the eastern part of the Taimyr Peninsula, Siberia, Russia (Text-fig. 1). The plant fossil studied is an aggregation of megastrobili, one of which is almost completely preserved (Text-fig. 2a). The mode of preservation of this fossil is a compression (phytoleima) with the well-preserved cuticles and in-situ seeds. Plant tissue impressions are visible on the rock matrix in places where the compressed plant material is detached.

The compressed material was macerated in concentrated nitric acid for a week. After using an ammonia solution for washing the oxidized coal, and further washing in distilled water, the obtained cuticles and the seeds were separated from the seed-bearing discs. In preparation for study, the cuticles were mounted in a glycerin-gelatin medium. A Carl Zeiss Axiostar digital optical microscope was used for visual examinations. Other cuticles were dried and mounted on mini-stubs for scanning electron microscopic study, using a JEOL JSM-6060A at the Faculty of Soil Sciences, the Moscow State University named after M. V. Lomonosov.
Triassic system in this section begins from the Keshinskaya and Tsvetkovomysskaya formations (Suits) of Induan age. Careful study of these deposits was done by A. S. Dagis and A. M. Kazakov (Dagis and Kazakov 1984).

The Keshinskaya Formation (lowermost part of the Induan stage) in this region consists of intercalated packets of shallow marine, lagoonal, and continental sandstones, siltstones and mudstones of green-grey, sometimes dark-grey and red-brown colour, with horizontal to cross-bedding lamination, with numerous calcareous and siderite concretions and pyrite nodules (Dagis and Kazakov 1984). The formation contains plant fossils, including mega-, meso- and microfossils, coal lenses, and small inter-beds consisting of coaly particles. Solitary foraminifers are reported from this formation as well (Dagis and Kazakov 1984, Kazakov et al. 2002). The conglomerates of 4 m thickness containing large pebbles occur at the base of the Keshinskaya Formation. This basal conglomerate consists of round pebbles of basalt porphyrite and diabases (dolerite or microgabbro) cemented by an iron-sand-clay terrigenic matrix. General thickness of the Keshinskaya Formation is about 150 m.

Plant megafossils occur practically everywhere in the Keshinskaya Formation. The most common elements of the Keshinskaya floristic assemblage are heterosporous isopetopsid lycopodiopsids Tomiostrombus nigayi (Schvedow) Sadovn., which are represented by rich monodominant localities (oriktocoenoses) of isolated sporophylls, small individuals of Pleuromeia sp., and peltasperms leave Lepidopteris arctica Mogutcheva (Mogutcheva 1980). Less frequent taxa found in rare locally separated loci (sublayers) only are equisetophytes Equisitites sixeliae Mogutcheva, ferns Cladophlebis borealis Pryn., C. parvulus Mogutcheva, C. cf. kirjamkensis Pryn., Sphenopteris cf. kirjamkensis Pryn., Kchonomakidium cf. srebrodolskiae Schivedow, cycadophytes Taeniopteris taimyrica Mogutcheva, female reproductive organs (ovuliferous discs) Peltaspermum sp., ginkgophytes Glossophyllum sp., Rhipidopsis sp., and isolated seeds Samaropsis sp., Carpolithes zwetkoviensis Mogutcheva (Mogutcheva 1980, 1996).

The plant fossil described below originated from the green-gray tuff-siltstones deposited in the lower part of the Keshinskaya Formation (Text-fig. 1, left), in close association with well-preserved leaves of various taxonomic affinity, which were not affected by any distant transportation, and were buried near the place where the parent plant grew. The taxa Taeniopteris taimyrica, Glossophyllum sp., Rhipidopsis sp. and others were found in the same locality as well (Mogutcheva 1980).

Systematic palaeobotany

Division Pinophyta REVEAL, 1996
Class Peltaspermopsidida CRONQUIST, 1981
Order Peltaspermales T.N.TAYLOR, 1981
Family Angaropeltaceae DOWELD, 2001 sensu
Naugolnykh 2012

Genus Taimrya NAUGOLNYKH et MOGUTCHEVA gen. nov.

Type gen. Taimyria triassica NAUGOLNYKH et MOGUTCHEVA gen. nov.
Plant Fossil Names Registry Number. PFN003026.

Derivatio nominis. From the Taimyr Peninsula.

Diagnosis. Long racemose aggregation forming cone or megastrobilus consisting of axis with peltate seed-bearing discs (which also can be interpreted as seed-bearing semi-closed capsules) with margins curved adaxially; disc round to ovoid, with short stalk connected at central adaxial part and attached to cone axis nearly perpendicularly in dense spiral pattern. Six to eight seeds concentrically displayed around stalk on adaxial surface of disc. Seeds platyspermic, ovoid, narrower at their apical micropylar end oriented toward disc stipe.

Comparison. The new genus differs from other closely related angaropeltian peltasperms (the genera Angaropeltum Doweld, Sylvocarpus Naugolnykh, Permoxylocarpus Naugolnykh) in the ovoid shape of the disc oriented across the megastrobilus/cone axis.

Taimyria triassica Naugolnykh et Mogucheva sp. nov.

Text-figs 2–11

Holotype. 4287/6, holotype figured here in Text-figs 2a, 3–10.

Plant Fossil Names Registry Number. PFN003027.

Repository. Monographic Department of the Geological Institute of Russian Academy of Sciences (Moscow, Russia).

During the study, the collection was kept in the Geological Institute of Russian Academy of Sciences (Moscow, Russia).

Derivatio nominis. From Triassic period.

Type locality. The Tsvetkov Cape locality, Taimyr, Siberia, Russia; Lower Triassic, Induan.

Diagnosis. Same as for the genus.

Description. Macromorphology. The specimen studied is represented by four megastrobili (marked by arrows on Text-fig. 2) preserved on one bedding surface. There is a thick axis on one side of the specimen (Ax in Text-fig. 2). The four megastrobili are located on both lateral side of the Ax axis, with two on each side. Therefore, one can suppose that the megastrobili were arranged on a fertile branch in pinnate order, or forming a pinnate frond-like structure. Two megastrobili are preserved almost completely. Since the actual attachment of the megastrobili to the same branch (Ax) is not clearly visible, only one of the strobili is selected as a holotype (Text-fig. 2a). Two other strobili preserved on the other side of the branch are not complete and show their basal parts only.

The most well-preserved strobilus (holotype) is of more or less cylindrical shape (Text-fig. 2a). It is about 61 mm long and 15 mm wide. The base of the strobilus is not visible. Second strobilus, which is also preserved almost completely, is very similar to the holotype, but somewhat narrower, 72 mm long and 12 mm wide.

Each strobilus consists of densely arranged seed-bearing megasporangiate discs attached to the common axis in spiral order and forming well-pronounced parastichy (Text-figs 3a, b, 4a, b). Each observed parastichus on one side of the strobilus has three seed-bearing discs. Thus, one complete cycle should include six discs. The holotype has eleven parastichy. The second, narrower megastrobilus has fourteen parastichy. Thus, each strobilus has more than seventy seed-bearing discs.

The possible fertile branch axis near the basal parts of the strobili is 7 mm wide and 80 mm long at visible part (Text-fig. 2, Ax). The surface of the axis is covered by very fine longitudinal ribs and furrows.

The seed-bearing discs are distinctly asymmetrical, ca. 5 × 9 mm in dimensions (Text-figs 2a, 3a, 4a, b). The long axes of the disc shields are oriented horizontally, and perpendicular to the main axis of the strobilus. This feature makes the present fossil different in comparison with other similar peltasperm female reproductive organs. The functionally upper or abaxial surface of the seed-bearing disc is smooth or slightly folded. Peripheries of the discs are entire-margined generally, but some discs bear six to eight unclear lobes about 1 × 2 mm in dimensions. Some discs demonstrate a flattened protective limb of about 2 mm wide at outer periphery of the lobes, making the disc semi-closed. This limb covers the seed base (Text-fig. 4b).

Cuticle preparations taken from the holotype show well-visible seed scars (Text-figs 3c, 4c). The seed scars are ovoid, 300 µm long and 200 µm wide on average. Size and shape of the seed scars well correspond to the size and shape of the chalazal base of the seeds. Judging from the material in hand, the seed scars were orientated along the radial directions of the seed-bearing disc.

The seeds are disposed beneath the seed-bearing disc and directly attached to the adaxial surface of the discs (Text-fig. 4b). The seed cuticles were extracted during the maceration of the discs (Text-figs 8–10).

The seeds are platyspermic, very small (according to the seed size ranking scale proposed by Artjushenko 1990). Seed are ovoid, 1.7–2.0 mm long and 1.0–1.2 mm wide, widest at the middle or lower one-third (Text-figs 8–10). The seeds are narrowed at the apical micropylar end. The seed peripheries are slightly flattened. The seed coat (spermoderm) is smooth, without distinct sculpture. The seed scarlet is about 300 µm in diameter, ellipsoidal to round, central in relation to the ventral side of the seed, somewhat impressed, surrounded by weakly developed ring-shaped uplifting (Text-figs 8b, 9a). The main axis of the seeds is straight to slightly curved. Since the seeds lack sarcotestal wings, we can conclude that the original plant had rather limited dispersal ability (autochorous or barochorous).

Very similar seeds, but considerably larger, were described as “Cordaicarpus” uralicus Kh.R.Dombr. from the lower Permian (Kungurian) deposits of the Cis-Urals (Dombrovskaya 1976). It was suggested that these seeds were produced by the peltasperm plant with the fronds Permocallipteris retensoria (Zaleskky) Naugolnykh and the seed-bearing discs Peltaspermum sp. (Naugolnykh and Kerp 1996, Naugolnykh 2014). Seeds of this type were found later in natural connection to the seed-bearing discs of Peltaspermum petaloides Naugolnykh (Naugolnykh 2016: 86, text-fig. 35A, B, D, pl. XXIX, 6).

Discovery of the present specimen, bearing seeds in natural connection to the seed-bearing discs similar to other representatives of Peltaspermales, supports the initial idea
that these seed forms belong to the peltasperms (Naugolnykh and Kerp 1996).

**Epidermal-cuticular structure.** The cuticles are relatively thick. The cell outlines are indistinctly pronounced.

The most well-preserved cell structure is observed on the adaxial cuticles, especially around the seed scars, where the cells are clearly visible and well-expressed in the cuticle relief (Text-figs 3c, 4c, 8–10).
The common epidermal cells are elongate, mostly of prolonged rectangular outlines, rarely more isometric. Average size of the cells is 40 × 70 µm. Radial cell walls are undulated to slightly curved. The straight cell walls are present as well. The periclinal cell walls are fairly smooth. The common epidermal cells form distinct rows radially disposed around the seed scars (Text-figs 3c, 4c). The cells become more isometric in the distance of 500–600 µm from the seed scar. Occasionally the papillae are joined into a common uplifting with weak extrusion (Text-fig. 7). Similar cutinization of the stomata is known for some other representatives of the order Peltaspermales (e.g., Naugolnykh 2005: figs 12–14, 16, 17). In very rare cases, a crescent-shaped uplifting is developed instead the papillae.
Text-fig. 5. Taimyria triassica Naugolnykh et Mogutcheva gen. et sp. nov., holotype 4287/6. a–d: epidermal-cuticular structure of upper surface of seed-bearing capsule. Locality: Tsvetkov Cape; Lower Triassic, Induan; Keshin Formation. Scale bar 100 μm (a, c, d), 50 μm (b).
Text-fig. 6. *Taimyria triassica* NAUGOLNYKH et MOGUTCHEVA gen. et sp. nov., holotype 4287/6. Epidermal-cuticular structure of upper surface of seed-bearing capsule. a–c, e–g: cuticles of upper surface of seed-bearing capsule, b – detail of (a), notice small white spot at picture center, which could be interpreted as scar of small monocellular trichome; d: conducting strand going to seed scar. Locality: Tsvetkov Cape; Lower Triassic, Induan; Keshin Formation. Scale bar 200 µm (a, c, d, g), 100 µm (e, f).
Common cells of the abaxial surface of the seed-bearing discs are of isometric outlines, round to polygonal, with average size 50 × 60 µm.

**Discussion**

The seed-bearing discs of *Taimyria triassica* gen. et sp. nov. are very similar to the general structure of the seed-bearing discs of *Sylvocarpus armatus* Naugolykh, which also belongs to the same family Angaropeltaceae (Naugolykh 2008). The main difference between genera *Taimyria* and *Sylvocarpus* Naugolykh is the horizontally-elongated proportions of the seed-bearing discs, which are characteristic of *Taimyria*. One more distinct feature of *Taimyria* is very long and narrow proportion of its strobilus. An additional character that makes *Taimyria* different from other peltasperm genera (with the exception of *Peltaspermum goniacanthus* Naugolykh and *Sylvocarpus armatus* Naugolykh) is a very small number of seeds per disc (not more than eight). The taxonomy and systematics of peltasperms in general, and the genus *Peltaspermum* T.M. Harris particularly, are used here in a traditional and canonical way (Stanislavsky 1976, Dobrussina 1980, Mogutcheva 1980, Meyen 1982, Gomankov and Meyen 1986, Durante 1992, Schweitzer and Kirchner 1998, Retallack 2002, Anderson and Anderson 2003). The modified “promoted” status of *Peltaspermum*, which could be recognized as having “natural” or botanical status (Poort and Kerp 1990), is more appropriate for usage in palaeoecological considerations only, not in taxonomic or floristic studies (for discussion see Naugolykh 2001, Holmes and Anderson 2005).

The gross morphology of the aggregations of strobili of *Taimyria triassica* is similar to the architecture of fertile branches of *Peltaspermum monodiscum* J.M. Anderson et H.M. Anderson from the Late Triassic deposits of the Molteno Formation (Anderson and Anderson 2003), but is different in a smaller number of seeds (11–12 seeds per disc for *P. monodiscum*, and 6–8 seeds for *Taimyria triassica*). Another difference between these two plants is a much deeper dissection of the megasporangiate disc, which is characteristic of *Peltaspermum monodiscum*.

During recent decades, a tendency to inadequately widening of the family Peltaspermaceae has developed. We believe that some chaos has developed in the entire Peltaspermales clade, because some genera were attributed to this family only based on limited information of leaves and/or some insufficient data on reproductive organs. According to the viewpoint of the present authors, only plants exhibiting the originally described flattened seed-bearing discs (= peltoids) of *Peltaspermum*-type can be reasonably assigned to the family Peltaspermaceae. The pinnate fronds of callipterids or their morphogenetic derivatives (such as lanceolate leaves of the genus *Parsongia* Zalesky and some other similar types) were typical of the plants belonging to the family Peltaspermaceae. For the identification and classification of lower taxa in the genus *Peltaspermum*, characters such as the number of seeds per one seed-bearing disc, the disc (= peltoid) margin morphology (smooth, festoon, lobed or others), the extent of the disc margin dissection into lobes (if any dissection took place), the extent and prominence of the radial sectors where seeds develop, can all be effectively used. The same character set can be useful for species definition in other genera attributed to other families of the Peltaspermales. On the basis of these characters, the genus *Peltaspermopsis Gomankov* was transferred to the synonymy of the genus *Peltaspermum* (see discussion in Naugolykh 2012).

Regarding the taxonomical diversity of Peltaspermales, it should be noted that only three families are recognizable in this order at present, i.e., Peltaspermaceae, Angaropeltaceae, and Vetlugospermaceae. The families Trichopityaceae S.V. Meyen and Unkomiaseae *Petriella* must be excluded from the order Peltaspermales, in contrast to the opinion expressed by Meyen (1987), because plants of these families have female reproductive organs of other types, and also because of their different anatomical structure, despite their sterile leaves appearing somewhat similar to the peltasperm s. I. leaves. For example, the gymnosperms with bipinnate seed-bearing lamina *Hamshawvia J.M. Anderson* et H.M. Anderson are now assigned to the family Hamshawviaceae J.M. Anderson et H.M. Anderson in the order Hamshawviales (Anderson and Anderson 2003).

To sum up, we insist that the order Peltaspermales should be used in its narrow taxonomical sense, otherwise this order will be transformed into a “trash-basket” for putting there any gymnosperm taxa of unclear affinity, poorly understood or even morphologically and anatomically misinterpreted.

The Peltaspermales can be phylogenetically traced back to the Carboniferous pteridosperms of the order Callystophytales (e.g., Meyen 1982, 1987). Later Mesozoic gymnosperms of the order Caytoniales (one of the possible “pre-anthophytes”) are sometimes regarded as phylogenetical descendants of the Peltaspermales (for discussion see Naugolykh 2008).
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Text-fig. 8. Taimyria triassica Naugolnykh et Mogutcheva gen. et sp. nov., holotype 4287/6. Structure of seed extracted from seed-bearing capsule. a, b: general morphology; c–e: detailed cellular structure. Locality: Tsvetkov Cape; Lower Triassic, Induan; Keshin Formation. Scale bar 1 mm (a, b; same scale for both figures), 100 μm (c–e).
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Text-fig. 9. Taimyria triassica NaugolnYkh et Mogutcheva gen. et sp. nov., holotype 4287/6. Structure of seed extracted from seed-bearing capsule. a: general morphology; b, c: detailed cellular structure. Locality: Tsvetkov Cape; Lower Triassic, Induan; Keshin Formation. Scale bar 1 mm (a), 100 µm (b, c).

Text-fig. 10. Taimyria triassica NaugolnYkh et Mogutcheva gen. et sp. nov., holotype 4287/6. a–f: seeds extracted from seed-bearing capsule. Locality: Tsvetkov Cape; Lower Triassic, Induan; Keshin Formation. Scale bar 1 cm.
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Text-fig. 11. Taimyria triassica Naugolnykh et Mogutcheva gen. et sp. nov. Suggested reconstruction of fertile shoot. Scale bar 1 cm.

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