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An advanced peltasperm *Permoxylocarpus trojanus* Naug. from the Lower Permian of the Urals (Russia): an ancient case of entomophily in gymnosperms?

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Summary: The evolutionarily advanced gymnosperm of peltaspermalean affinity *Permoxylocarpus trojanus* Naug. from the Lower Permian deposits of the Urals (Russia) is described. Female reproductive organs of *P. trojanus* are spherical, semi-closed, peltate capsules with 15–16 enclosed seeds. Both macromorphology and microstructure, including epidermal-cuticular characters and the anatomical structure of conducting tissues, are characterized. Sterile leaves of *Praephylladoderma leptoderma* Naug., provisionally belonging to the same parent plant, are also described. Some aspects of peltasperm evolution during the Late Palaeozoic–Early Mesozoic are briefly summarized. The occurrence of enclosed ovuliferous organs (capsules) in some peltasperms, the structure of their pollen grains as well as some palaeoentomological evidences suggest the gradual shift from anemophily to entomophily in evolution of these gymnosperms.

Keywords: peltasperms, evolution, Permian, seed-bearing organs, preangiosperms, fossil records, entomophily

Pteridosperms sensu lato were widely distributed seed plants during the Late Palaeozoic. This very diverse group is commonly regarded as a grade rather than a well-supported clade. Despite that, a general evolutionary pattern of this group can be recognized entailing the morphology of the fertile organs.

The most ancient pteridosperms known from the Upper Devonian (Lagenostomales: *Elkinsia polymorpha, Moresnetzia zalesskyi* and some other related forms; Rothwell & Serbet 1992; Serbet & Rothwell 1992; Krassilov 1995; see these papers for further references) had relatively simple fertile fronds or monopodially branched shoots without extended leaf lamina. Their ovules and/or ovulate cupules were attached to the branch tips. Further pteridosperm evolution entailed the development of fertile fronds which were very similar or almost identical to the ordinary vegetative fronds, but with the ovules attached to the leaf lamina or frond rachis (Trigonocarpales, Callystophytales; Stidd 1981; Retallack & Dilcher 1988; see these papers for further references). Pteridosperms of this grade were common in Carboniferous vegetation, especially in the equatorial belt.

During the Permian, the pteridosperms became widely distributed, more diverse and advanced than their Carboniferous members. Within these plants, the modified fertile fronds with reduced leaf laminae were gradually transformed into specialized ovuliferous organs. In some taxa (belonging mainly to the order Peltaspermales), these organs provided better protection for the ovules, partially covered by the derivates of leaf lamina (i.e., ‘cupules’ and capsules of different kinds). Peltaspermalean pteridosperms or peltasperms probably gave rise to the Mesozoic pteridosperm orders Corystospermales and Caytoniales. Caytoniales are often regarded as ‘preangiosperms’

(Harris 1951; Doyle 1978; Dilcher 1979; Krassilov 1984; etc.). Ovuliferous organs of corystosperms can be interpreted as modified megasporophylls (Crane 1988) that originated from the fertile fronds of primitive pteridosperms. The ovules of many Mesozoic pteridosperms, or at least some of them (e.g., *Petriellaea* Taylor et al., *Caytonia* Harris; see for review: Taylor & Taylor 2009) were almost completely enclosed by modified capsules, linking these plants morphologically close to the angiosperms.

Permian peltaspermalean pteridosperms may have linked to the relatively primitive Carboniferous and progressive Mesozoic forms, and because of this intermediate position they are of special palaeobotanical interest. Permian peltaspermalean pteridosperms possessed a unique syndrome of mixed characters represented by peltate, discoid, seed-bearing organs aggregated into racemose structures, and pinnate or simple leaves (Fig. 1). Therefore, this group is important for understanding the evolutionary trends in gymnosperms and other seed plants.

In the present paper, new peltaspermalean pteridosperm material collected from the Lower Permian deposits of the Urals (Russia) is described. The plant characterized here was attributed to the order Peltaspermales, family Angaropeltaceae, and named *Permoxylocarpus trojanus* Naug. Original description of the material was published in Russian only, with the exception of an English diagnosis (Naugolnykh 2007), as it is required by the International Code of Botanical Nomenclature. This plant shows some characters that are more typical of Mesozoic 'preangiosperms' rather than of Palaeozoic pteridosperms. In addition to the general morphological observations, some anatomical and epidermal-cuticular characters of the plant were studied. Comparison were drawn between *P. trojanus* and the most closely related taxa among morphologically similar Permian and Triassic plants, i.e., *Peltaspermum* Harris, *Angaropeltum* Doweld, *Caytonia* Harris, *Umkomasia* Thomas, *Spermatocodon* Thomas, *Pilophorosperma* Thomas, *Petriellaea* Taylor et al., and *Ktalenia circularis* Archangelsky.

Materials and methods

The main part of the material studied was collected from Chekarda-1 locality (Kungurian of the Cis-Urals, Perm district, Russia) by the first author during several field seasons in 1988–1996. The holotype of *Permoxylocarpus trojanus* Naug. was provided by the late Prof. P.A. Sofronitsky (Perm State University). Some additional specimens were collected at the Chekarda-1 locality by A.G. Sharov (Palaeontological Institute, Moscow) in 1959–1960 and provided by A.V. Gomankov (Komarov Botanical Institute, St. Petersburg). One specimen from the V.A.Tsimbal collection (Moscow; TC/P-1; Fig. 3E) was also studied. For exact position of the plant-bearing strata cited in the text, see Naugolnykh (1998, 2007). Specimens characterizing the Upper Permian peltasperms of Pechora coal basin (Fig. 1A, C–F) were provided by S.K. Pukhonto (State Vernadsky Geological Museum, Moscow); the racemose aggregation of seed-bearing discs (Fig. 1C) from the Upper Permian of Russian Far-East was given to the authors by V.I. Burago (Vladivostok).

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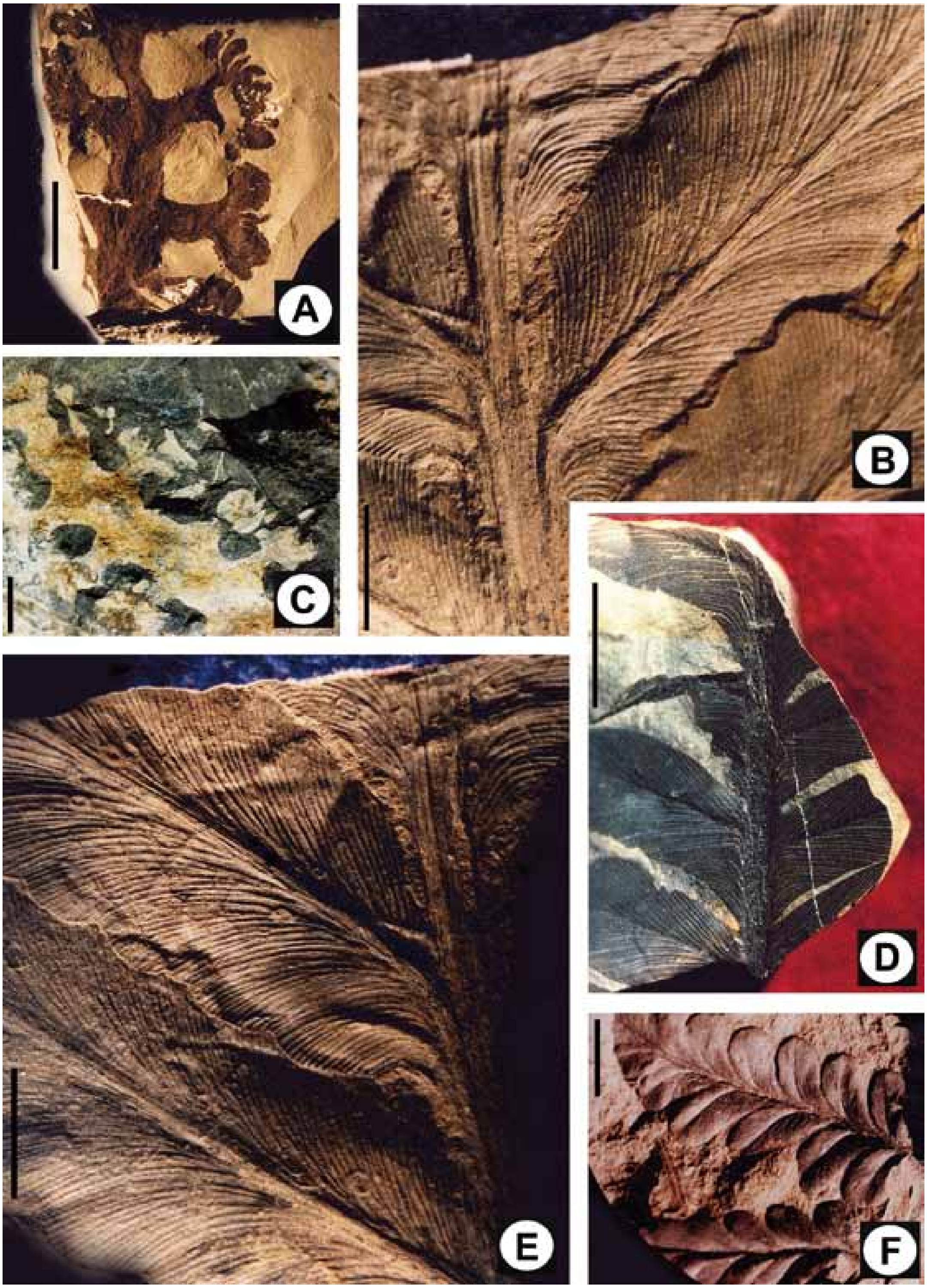
Figure 1. A – *Peltaspermum* sp., a racemose aggregation of seed-bearing discs found in close association with leaves of callipterid morphology; Talbeiskian Formation, Urzumskian stage, Upper Permian; Pechora coal basin, Adzva River, outcrop 1027-A – 679. B, E – *Comia* sp., leaf with unicoherent venation; Seidinskian Formation, Kazanian stage, Upper (Middle) Permian; Pechora coal basin, Syr-Yaga River, Verkhesyryaginskoe locality. C – *Peltaspermum buragoae* Naug. (in manuscr.), a racemose aggregation of seed-bearing discs found in close association with leaves of callipterid morphology; Sitza floristic assemblage; Ugodinzinskian Formation, Kazanian stage, Upper Permian; central part of



Primorie, Russian Far-East, Sinegorka River, left bank of Kamenisty spring. D – *Rhachiphyllum* (= *Callipteris*) *adzvense* (Zalessky) Naug., last order pinna; Seidinskian Formation, Kazanian stage, Upper (Middle) Permian; Pechora coal basin, Syr-Yaga River, Verkhesyryaginskoe locality. F – *Rhachiphyllum* (= *Callipteris*) *adzvense* (Zalessky) Naug., two last order pinnae; Seidinskian Formation, Kazanian stage, Upper (Middle) Permian; Pechora coal basin, Nizhne-Syryaginskoe locality, borehole NSK-218, depth 156,2 m. Scale bar = 1 cm.

The specimens were macerated in the Schulze's reagent according to standard procedure (Kerp 1990), and the cuticles obtained were studied by means of the light microscope PZO and the Stereoscan 600 scanning electron microscope (Cambridge).

Terminology

'Cupule' is a commonly used term for the description of closed or semi-closed derivates of planate seed-bearing structures. This term is ambiguous, however, in relation to different representatives of Trigonocarpales, Peltaspermales, Caytoniales and some other groups of gymnosperms, whose cupule-like organs of independent origin may not be considered as homologues. Because of that, we prefer to use term 'capsule' instead of 'cupule' for any closed or semi-closed ovuliferous organs of gymnosperms. This term is well-defined morphologically, but it is not loaded by phylogenetic connotations. The term 'capsule' was used by Meyen (1984) in a very similar way.

Results

Peltaspermales Taylor, 1981
Angaropeltaceae Doweld, 2002
(= Cardiolepidaceae S. Meyen, 1977, emend. 1979; nom. illeg.)

***Permoxylocarpus* Naugolnykh, 2007.** Female generative organs are spherical capsules, with central stalk and with seeds disposed inside the capsule. Outer surface of the capsule bears radial ribs.

The genus differs from the most closely related genera *Sylvocarpus* Naug. and *Angaropeltum* Doweld (= *Cardiolepis* Neuburg, nom. illeg.) in showing well developed radial ribs disposed on the surface of the capsule; from *Ktalenia* Archangelsky in a considerably larger number of enclosed ovules (15–16 instead of 1–2) and also in another type of associated leaves (lanceolate leaves with the parallel venation of *Praephylladoderma leptoderma* Naug., instead of pinnate leaves of *Ruflorinia sierra* Archangelsky); from *Petriellaea* Taylor et al. in more numerous ovules per capsule (15–16 instead of 5–6) and in the central position of the capsule stalk (stalk or pedicel of *Petriellaea* attached to the side part of the cupule); from the corystosperm ovulate organs belonging to *Umkomasia* Thomas and closely related genera in having more numerous ovules (15–16 instead of 1–2 per ovuliferous organ), and also in the position of the stalk (central for *Permoxylocarpus* and marginal for *Corystospermum, Umkomasia* and related forms like *Pilophorosperma*). Associated leaves of *Permoxylocarpus* and corystosperms are also very different, such as simple lanceolate leaves of *Praephylladoderma*, provisionally linked to *Permoxylocarpus*, and compoundly pinnate leaves of *Dicroidium* (characteristic of corystosperms). There is a certain similarity between *Permoxylocarpus* and *Caytonia* cupules. The most important difference between these genera is the position of the stalk which is central for *Permoxylocarpus* and marginal for *Caytonia.* Moreover, *Caytonia* had compound leaves of *Sagenopteris* type with the net venation whereas *Permoxylocarpus* had simple lanceolate leaves.

***Permoxylocarpus trojanus* Naugolnykh.** Semiclosed capsules spheroid, with umbrella-shaped peltate round lamina on central stalk. Marginal parts of the lamina strongly turned downward. Outer surface of the capsule bears smooth radial ribs disposed around the place of the stalk attachment. Ovoid areas between the ribs probably corresponding to the places of seed attachment (seed scars). Surface of the capsule, which is more distant from the stalk, is smoother or bears unclear concentric folds. Each capsule bears 15–16 seeds located inside the capsule and surrounding the central stalk. Some seeds could be immature because of the asymmetrical shape of the capsule.

The collection studied includes six capsules (Fig. 2; Fig. 3) attributed to this species. The mode of their preservation is compression/impression. Some parts of compressed material are missing, therefore, one can see the imprint of the outer surface of the generative organ.

The holotype (Fig. 2A; Fig. 3B) exposed from its adaxial surface has a slightly deformed asymmetrical spheroid shape. Other specimens have same macromorphological features, but some of the capsules (Fig. 2D; Fig. 3A, C) expose their adaxial surface (like the holotype), and others show their abaxial surface (Fig. 2B; Fig. 3D, E).

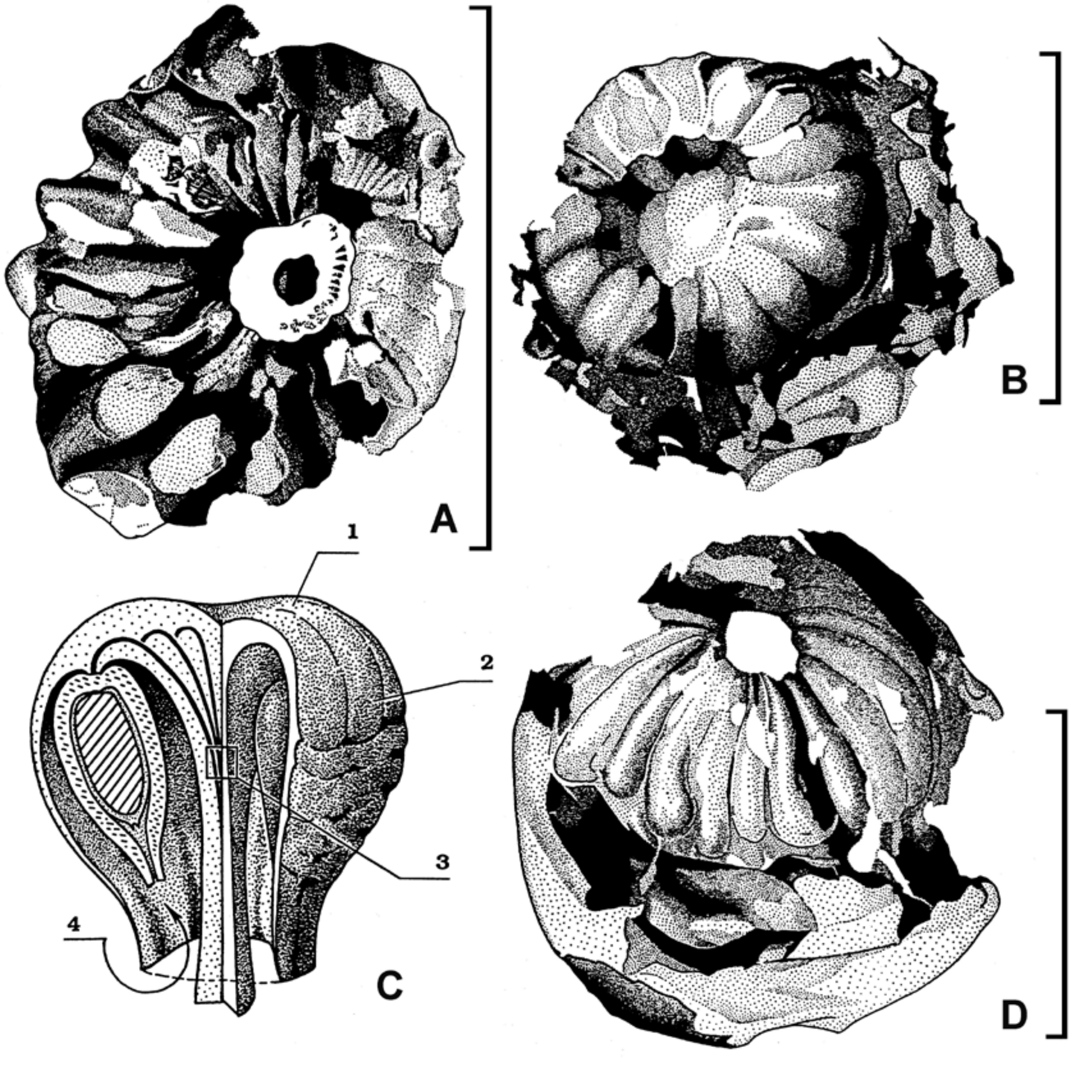


Figure 2. A, B, D – macromorphology of *Permoxylocarpus trojanus* Naug., seed-bearing capsules (A – holotype 3773(11)/244(91); Krutaya Katushka locality; B, D – syntypes; Chekarda-1 locality, layer 10; Koshelevskian Formation, Kungurian stage, Lower Permian; Sylva River Basin, Perm region). C – general morphology of angaropeltidian seed-bearing capsule: 1 – abaxial surface; 2 – radial rib; 3 – stalk with conducting tissues; 4 – way for pollen grains to seed micropyle. Scale bar = 1 cm.

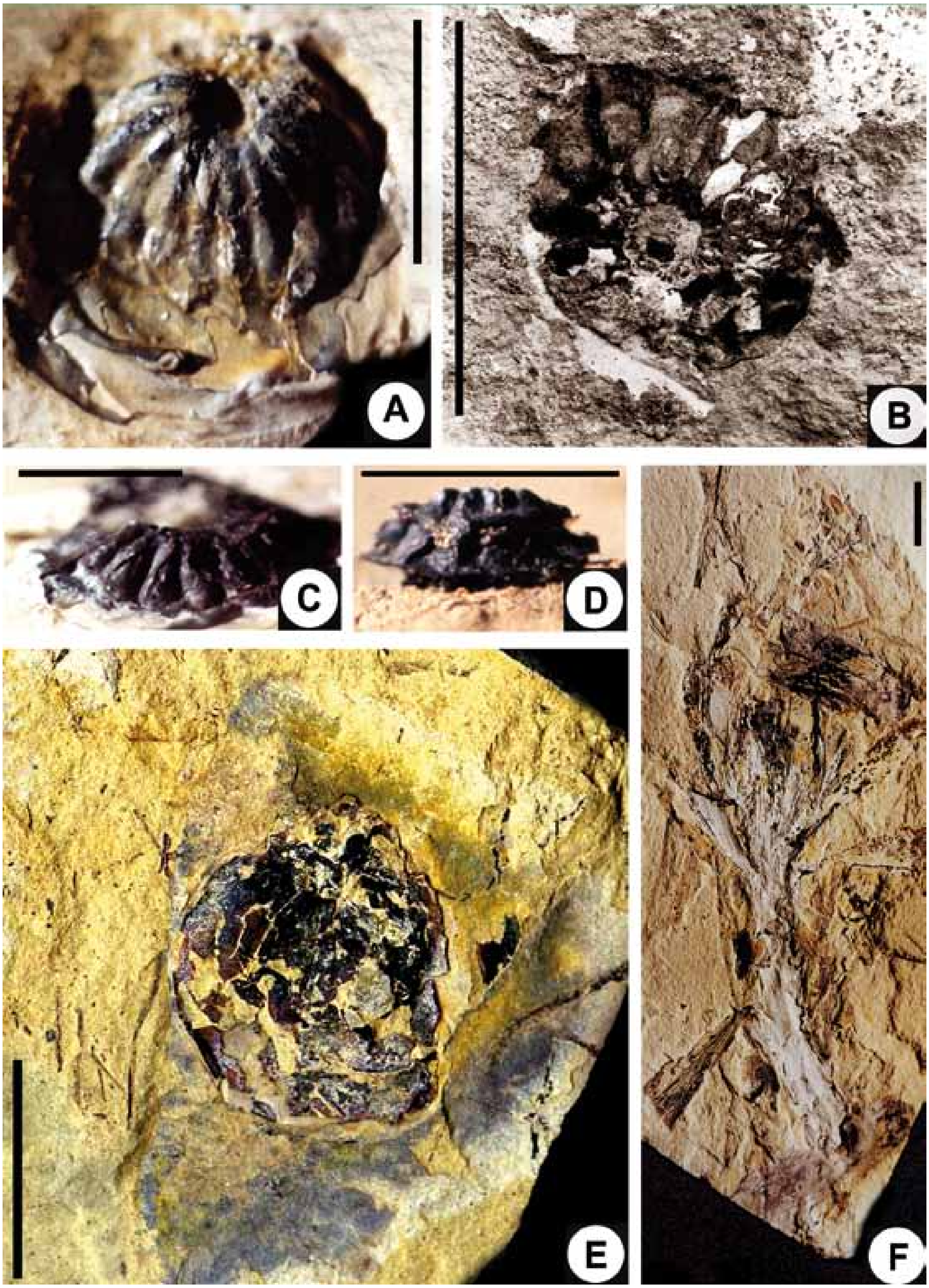


Figure 3. A–E – macromorphology of *Permoxylocarpus trojanus* Naug., seed-bearing capsules (B – holotype 3773(11)/244(91); Krutaya Katushka locality; A, C, D – syntypes; E – specimen from V. A. Tsimbal collection, TC/P-1; Chekarda-1 locality, layer 10; Koshelevskian Formation, Kungurian stage, Lower Permian; Sylva River Basin, Perm region). F – *Praephylladoderma leptoderma* Naug., leafy shoot; Chekarda-1 locality, layer 10; Koshelevskian Formation, Kungurian stage, Lower Permian; Sylva River Basin, Perm region. Scale bar = 1 cm.

There is a small unclear round depression at the capsule's upper part. This depression corresponds to the place of the stalk attachment (Fig. 2B, C). The adaxial surface of the capsule has nearly 15 alternating smooth furrows and wide radial ribs. The ribbed surface forms the first concentric band closest to the stalk. The next concentric band being farther away from the stalk and located nearer the outer margin of the capsule is separated from the previous band (bearing the lobes) by the well-developed definitive fold. The fold is represented as a concentric rib on the abaxial (outer) surface of the fructification. This second band bears poorly developed concentric and radial folds. Next, the most outer band (third band) forming margins of the capsule has a smoother surface than the second band. There is one more fold between the second and the third concentric band of the capsule. This fold corresponds to the place of curving of the capsule's 'umbrella'. The lower (adaxial) surface of the capsules is covered by radial ribs. The margin of the capsule is entirely smooth.

The capsule is spherical, with the margins of the capsule's 'umbrella' directed downwards. Postdiagenetic compression of the sediment leads to a flatter and smoother shape of the fructification. The original form of the capsule was more three-dimensional, almost regularly spherical. Ovules disposed inside the capsule and places of their attachment correspond to the lobes of the first capsule band. The ovules surround the stalk of the capsule in a radial arrangement (Fig. 2C).

Anatomical structure of conductive tissue. A piece of the capsule pedicel of the holotype was macerated. Numerous tracheids of the conductive bundle were extracted and studied using SEM (Fig. 4A–C, F). Two types of tracheids were distinguished. Some tracheids are narrow (their diameter 7–15 µm in transsection), with helical thickenings on the cell walls (Fig. 4B–C). The tracheids of another type are wider (15–20 µm in diameter), with circular or oval bordered pits (diameter of their borders is ca. 7–8 µm) arranged in opposite to alternate pattern into 2 (rarely 3) vertical rows on lateral cell walls (Fig. 4A), sometimes co-occurring with helical (Fig. 4C) or reticular (Fig. 4F) thickenings. Probably, the narrow tracheids of the first type belonged to protoxylem whereas the wide ones were taken from metaxylem.

Epidermal-cuticular structure of the capsule. Cuticles from the three different areas of the capsule shown on Fig. 2D and Fig. 3D were studied. Each area has its own specific cuticular characters.

Cuticles of the first type were taken from the lower part of the capsule, near the margin of the capsule (Fig. 4E, G). The cuticle is relatively thick, with numerous cells of isometric outlines, mostly hexagonal. At the central part of almost every cell there are small papilla-like structures with shallow folds or depressions on the uplifting top. Average diameter of the cells is 15–25 µm, sometimes slightly more.

Cuticles of the second type were taken from the outer side part of the capsule. This cuticle is also quite thick, robust, with well developed polygonal epidermal cells of prolonged outlines (Fig. 4D, H). Cell size is 15×30 µm in average. Papillae or stomata were not found. Similar cuticles are known for *Phylladoderma tscheremuschca* Esaulova from the Lower Tatarian (Urzhumskian) of the Volga River basin (close vicinity of Kazan, right bank of the Volga River, Pechischi village, Cheremushka outcrop: Esaulova 1998: Pl. IX), and *P. sentjakensis* Esaulova from the Lower Kazanian, (Sentjak village, Kama River: Esaulova 1986: Pl. XIV, XV).

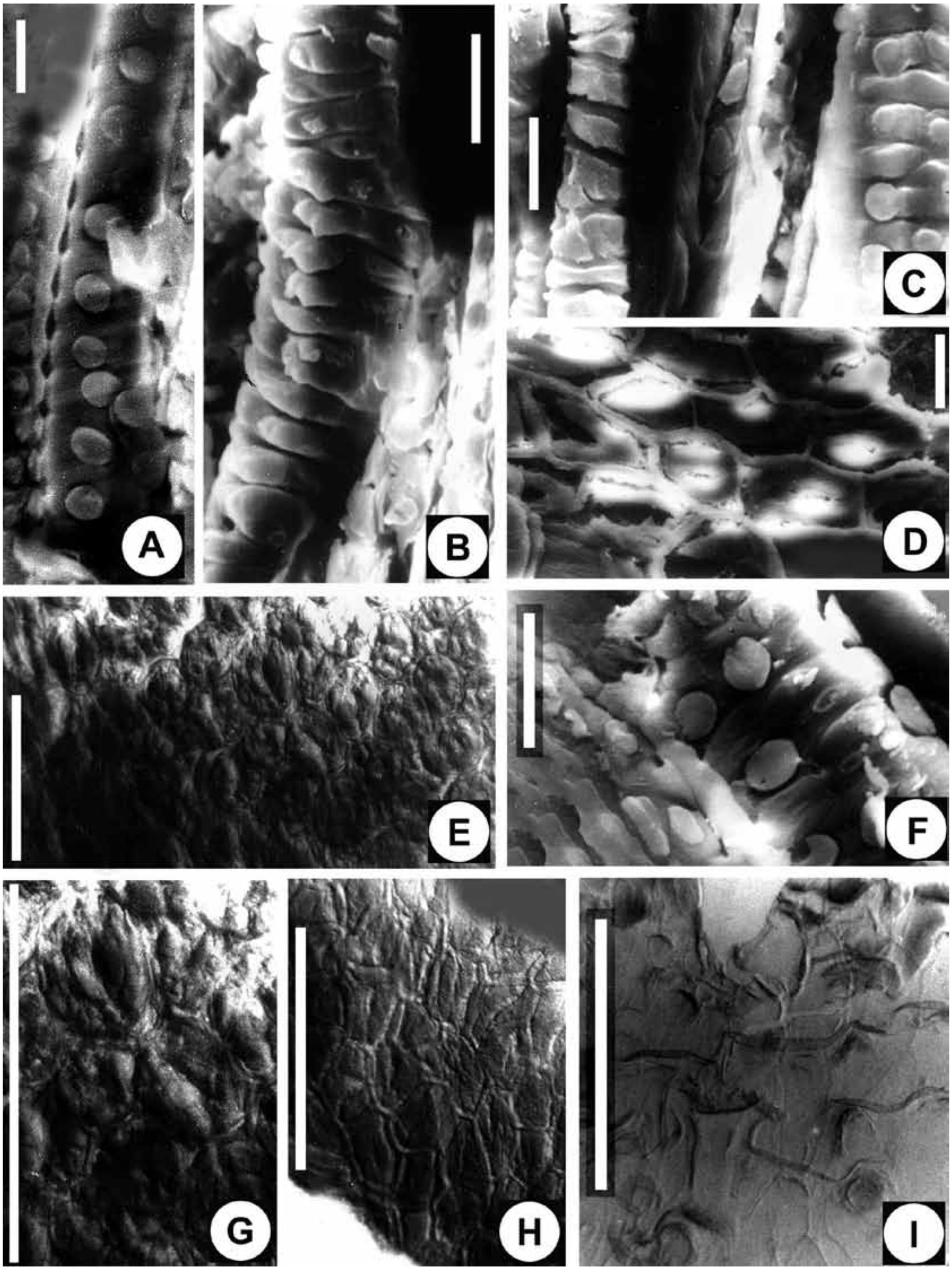


Figure 4. Anatomy of *Permoxylocarpus trojanus* Naug., seed-bearing capsules (preparation was made from the specimen shown on Fig. 2D and Fig. 3A). A – wide tracheid with circular bordered pits; B – narrow tracheid with helical to reticulate thickenings; no bordered pits; C – narrow tracheid with helical thickenings (left) and wide tracheid with circular bordered pits and helical thickenings (right), F – wide tracheid with circular bordered pits and reticular thickenings; D, E–I – epidermal-cuticular structure. Chekarda-1 locality, layer 10; Koshelevskian Formation, Kungurian stage, Lower Permian; Sylva River Basin, Perm region. Scale bar = 10 µm (A–D, F), 100 µm (E, G–I).

Cuticles of the third type were taken from inner surface of the capsule. These cuticles are very thin; only some weakly preserved cell walls are seen (Fig. 4I). Surface of the cuticle is relatively smooth, with some small, but distinct papillae.

Associated organs. The Kungurian floristic assemblage with *Permoxylocarpus trojanus* is taxon-rich (Zalessky 1937, 1939; Naugolnykh 1993, 1998). Several whole-plant-concept reconstructions have been proposed for some of the Kungurian higher plants. The best documented taxa from these deposits are: *Sadovnikovia belemnoides* Naugolnykh (sporophylls) / *Viatscheslaviophyllum* sp. (phylloids) [lepidophyte] — *Bowmanites biarmensis* Naugolnykh (strobiles) / *Sphenophyllum biarmicum* Zalessky (sterile leaves and stems) [sphenophyll] — *Equisetinostachys* sp. (fertile zones and sporophylls) / *Phyllotheca stenophylloides* Zalessky (sterile leafy shoots), *Sachyogyrus multifarius* Zalessky (fertile stems and sporophylls) / *Phyllotheca biarmica* Zalessky (sterile leafy shoots) [sphenophytes] — *Ptychocarpus distichus* Naugolnykh (fertile fronds) / *Pecopteris uralica* Zalessky (sterile fronds) [marattialean fern] — *Alternopsis stricta* Naugolnykh (ovuliferous organs and specialized fertile (?) leaves) / *Psygmophyllum cuneifolium* (Kutorga) Schimper (sterile leaves) [pteridosperms] — *Rhachiphyllum* (al. *Callipteris*) *retensorium* (Zalessky) Naugolnykh (sterile fronds) / *Peltaspermum* sp. (ovuliferous organs – seedbearing discs) / *Permotheca disparis* (Zalessky) Naugolnykh (polliniferous organs) [peltaspermalean pteridosperms] — or *Peltaspermum retensorium* (Zalessky) Naugolnykh & Kerp (1996), species, promoted to the natural status; *Gaussia imbricata* Naugolnyh (ovuliferous organs) / *Rufloria* spp. (normal well developed leaves) / *Nephropsis* (*Sulcinephropsis*) *crinitus* Gluchova (bracts) — *Scirostrobus pterocerum* (Naugolnykh) Doweld et Naugolnykh (ovuliferous organs) / *Sylvella* sp. (seeds) / *Rufloria* spp. (normal well developed leaves) / *Nephropsis* (*Sulcinephropsis*) sp. (bracts) / *Lepeophyllum* sp. (short scale-like leaves) [vojnovskyaleans]. The two last mentioned reconstructed whole-plant-concept taxa are probably ecological varieties or morphs of one and the same natural species. Thus, a general type of the associated sterile leaves is known for almost all generative organs of the most common plants of the flora.

If generative organs are found, the sterile leaves belonging to the same plant are already present in collections containing many plant megafossils collected from one and the same locality. This corresponds to the so-called 'Harris-rule', which is often cited in palaeobotanical literature and is based on the simple empirical observation that commonly each plant produces many more sterile leaves than generative organs.

In the case of *Permoxylocarpus trojanus*, we can also use a typological model as a base for reconstruction of relationship between different organs. For such a model we can use some closely related forms belonging to the same taxonomic group, e.g., *Angaropeltum* (*Cardiolepis,* nom. illeg.) from the slightly younger deposits (Kazanian) of the Russian platform and Cis-Urals. All of the earlier described species of *Angaropeltum* (*A. piniformis* (Neuburg) Doweld, *A. sentjakensis* (Esaulova) Doweld) had the sterile leaves of *Phylladoderma* type. However, leaves of this type have never been described from the Kungurian of the Cis-Urals before. Hence, after careful reinvestigation of the previously collected material and additional field work, the sterile leaves of the Kungurian phylladodermas were found. They are described below and attributed to *Praephylladoderma leptoderma* Naug. Most probably, these leaves belonged to the same parent plant as those of *Permoxylocarpus trojanus.*

***Praephylladoderma* Naugolnykh.** Strap-like narrow leaves with wedge-like base and round apex (Fig. 3F). Venation parallel, veins robust at the leaf base, but narrower in the leaf apex. Two main veins emerging from the leaf base. Veins never come out to the leaf margins. Veins always bifurcating three to four times, simple veins are absent. Leaf lamina very thin, unresisting to maceration. Epidermal structure is unknown. This genus differs from the most closely related genus *Phylladoderma* Zalessky in very narrow leaf lamina and thin cuticles unresistent to maceration in Schulze's reagent.

Species composition: type species *P. leptoderma* Naug. and probably some undescribed forms from the Ufumian and lowermost Kazanian of the Cis-Urals and Kama-Volga Rivers basin.

***Praephylladoderma leptoderma* Naugolnykh.** Long, narrow lanceolate leaves superficially similar to *Cordaites*, but having another pattern of venation. Leaves simple, linear, with wedge-like narrow base. Maximal width of the leaf disposed near its apex. Leaf apex round; apexes of the young undeveloped leaves can be slightly acute. Venation regularly dichotomous; proximal parts of veins robust, middle and apical parts of the veins rather thin. Two distinctive basal veins entering the leaf base. Each vein dichotomously branching up to four times. Average length of the leaves is 9–10 cm; average width of the leaves is 1 cm. There are four leafy shoots in the collection studied. One of them is shown on Fig. 3F. They possess leaves, preserved in organic connection to the shoots. Leaves arranged in loose spiral order. Place of leaf attachment marked on the shoot by small uplifting having a small subtriangular scar of the leaf attachment in its upper part.

Discussion

The plants most similar to *Permoxylocarpus trojanus* are *Sylvocarpus armatus* Naug. (Naugolnykh 2008a) and *Angaropeltum* Doweld, such as *A. piniformis* (Neuburg) Doweld, initially described by Neuburg (1965) and later reinterpreted by Meyen (1977, 1979, 1984), as well as the closely related, but less known species *A. sentjakensis* (Esaulova) Doweld. The most important difference between *Sylvocarpus* and *Permoxylocarpus* is the absence of radial ribs for the first genus and its almost completely closed seed-bearing capsule. *Angaropeltum piniformis* is a characteristic species for Kazanian of the Pechora Cis-Urals.

Female generative organs of *A. piniformis* are spherical capsules enclosing numerous seeds of *Nucicarpus* Neuburg type. The seeds are also very distinctive and characterized by long and narrow micropylar parts. The stalk of the capsule is attached to its adaxial surface at the center. Thus, the general structure of both *A. piniformis* and *Permoxylocarpus trojanus* is very similar. The only important difference is the presence of the well-developed sculpture of the *Permoxylocarpus trojanus* capsule's surface, consisting of the above mentioned radial ribs and furrows as well as a stronger vascularization and a smaller size of the *P. trojanus* capsules. Sterile leaves of *A. piniformis* (*Phylladoderma* Zalessky) and *P. trojanus* (*Praephylladoderma* Naug.) are basically very similar, too. *A. piniformis* and some poorly documented forms from the Ufimian (Roadian) of the Cis-Urals may be regarded as evolutionary descendants of *P. trojanus.*

A very similar pattern of macromorphological characters is known for another gymnosperm *Ktalenia circularis* Archangelsky. This species originates from the Early Cretaceous of Santa Cruz Province in Argentina. *K. circularis* has ovuliferous capsules, which were also previously described as cupules attached to the fertile axis in opposite order, probably at the basal area of several linear bracts (Archangelsky 1963; Taylor & Archangelsky 1985). One or two ovules were present in each capsule. The short undeveloped pedicel of the capsule appears to be lateral, i.e., attaching to the capsule's lateral side.

The most notable difference between *K. circularis* and *Permoxylocarpus trojanus* is the considerably greater number of seeds/ovules which are present in the latter species. The type of associated leaves is also very different. *Ktalenia circularis* had sterile tripinnate fronds of *Ruflorinia sierra* Archangelsky, in contrast to the simple lanceolate leaves of *Praephylladoderma leptoderma,* which probably belong to the plant with the capsules of *Permoxylocarpus trojanus.*

Another plant, which is morphologically similar to *Permoxylocarpus trojanus*, has been described from the Triassic of Antarctica (Taylor et al. 1994) as *Petriellaea triangulata* Taylor, DelFueyo et Taylor. Female generative organs of *P. triangulata* were interpreted as small cupules with vascular strand of reticulate-scalariform tracheids in the stalk (pedicel), dividing into discrete five or six bundles run to the ovules. The ovules are arranged into a single oblique row or two rows inside the cupule. These ovules are small (1.5×1 mm) and ovoid (Taylor et al. 1994), similar to the Angaran *Nucicarpus.* The most important difference between *P. triangulata* and *Permoxylocarpus trojanus* is the asymmetrical position of the cupule pedicel of *P. triangulata* attached to the side part of the cupule. Anoter difference is the smaller number of seeds incapsulated in the cupule of *Petriellaea triangulata* and the smaller size of the cupule (homologous organ to the *Permoxylocarpus trojanus* capsule).

There are some characters in common between *Permoxylocarpus* and *Caytonia* (Thomas 1925). The latter genus was studied in detail by excellent works of Harris (1933, 1940, 1951, 1958). The basic similarity between *Permoxylocarpus* and *Caytonia,* i.e., general shape of the capsule, as well as similarity of *Permoxylocarpus* with some other Mesozoic pteridosperms, especially of the Corystospermaceae family, shows that these groups can be regarded as one grade in pteridosperm evolution. Tracheids with bordered pore-pairs as known for *Caytonia* (Reymanowna 1970, 1973) are similar to the tracheids of *Permoxylocarpus.*

The most important differences between Permian *Permoxylocarpus* and *Angaropeltum* on the one hand, and Mesozoic *Corystospermum, Umkomasia* (and other related corystosperm taxa based on seed-bearing organs), *Caytonia, Petriellaea*, and *Ktalenia* on the other hand, are the mode of the stalk attachment as well as the general shape of exostomium (i.e., the aperture for penetrating of pollen grains inside the capsule). *Permoxylocarpus, Sylvocarpus,* and *Angaropeltum* had a central stalk, with the ovules attached to the adaxial surface of the capsule in radial order. Like *Caytonia, Corystospermum, Umkomasia, Petriellaea*, and *Ktalenia*, they had a marginally disposed stalk and the ovules of the latter two genera were attached to the internal surface of the incurvated lamina-like seed-bearing capsule, enclosed to a different extent (semi-closed or even almost open for *Corystospermum* and *Umkomasia* and almost completely closed for *Petriellaea, Caytonia,* and *Ktalenia*). The exostomium of *Permoxylocarpus* and *Angaropeltum* was circular and distinctly larger, the one of *Sylvocarpus* was split-like, the one of *Caytonia* was semi-lunar, and it was rounded in *Ktalenia. Corystospermum* and *Umkomasia* had no exostomium at all because of a reduction of the capsule and rather large ovules. In general, all the forms listed above show a pattern characterized by a decrease in seed number and reduction of the capsule size.

Evolutionary predecessors of the angaropeltidians were representatives of Peltaspermaceae recorded from uppermost Carboniferous and Lower Permian deposits (Meyen 1984; Naugolnykh 2007).

These plants had open peltate seed-bearing discs, which most probably were wind-pollinated. The evolution of female reproductive organs in the peltasperms appears as a gradual transition from the open discs to almost enclosed capsules (Meyen 1984) which provide additional protection for ovules (Naugolnykh 2009). This trend shows a certain resemblance to the transformations of pistilate inflorescences from simple spikes and globose heads to disc-shaped inflorescences in the tribes Dorstenieae and Castilleae, and then to the enclosed syconia in the tribe Ficeae of the angiosperm family Moraceae (Datwyler & Weiblen 2004; Clement & Weiblen 2009). Fig-like flowers with enclosed perigone formed by completely connate tepals are also found in *Aspidistra locii* Arnautov & Bogner belonging to the family Convallariaceae (Bogner & Arnautov 2004). Although the seed-bearing organs of peltasperms are not homologues of the angiosperm flowers or inflorescences, we may compare them as organs of similar functions.

Within extant plants, the capsule-like female reproductive organs occur only in taxa which are highly specialized in pollination by arthropods, like fig wasps of the family Agoninae in *Ficus* (Weiblen 2004) or soil amphipods or collembolans in *Aspidistra* (Conran & Bradbury 2007). It is no wonder because these enclosed organs obstruct access for wind-dispersed pollen to the ovules. As molecular phylogenetic reconstructions show, the shift from anemophily to entomophily in Moraceae is nearly associated with the transition from globose to disc-shaped inflorescences and to syconia (Datwyler & Weiblen 2004; Clement & Weiblen 2009). Certain functional similarity of seed-bearing capsules in the peltasperms with such structures as syconia of *Ficus* and the enclosed perigone of *Aspidistra locii* suggest that evolutionary transformations of female reproductive organs in these extinct gymnosperms were attended with their shift to insect pollination. Although the microstrobiles of peltasperms does not show evident traits of entomophily, this condition (the male generative organs which indicate wind pollination) occur in some extant plant taxa pollinated by insects, e.g., in *Brosimum*, a member of Moraceae (Datwyler & Weiblen 2004).

This hypothesis is in good agreement with the evidences of close interactions between peltasperms and insects. Peltasperm pollen were found in guts of some Permian insects (Krassilov & Rasnitsyn 1997), and the microsporangia with the wall perforations and bites made by insects occur on the microsporangium walls in some peltasperms (Naugolnykh 1998). The seed-bearing capsules damaged by insects are also known in some Angaropeltidaceae (Naugolnykh 2008a, b).

Moreover, the gradual shift from anemophily to entomophily in peltasperms can be indirectly confirmed by correlation between the structure of their female reproductive organs and the types of pollen grains. The early Permian peltasperms *Autunia conferta* (Sternberg) Kerp and *Peltaspermum retensorium* (Zalessky) Naugolnykh & Kerp had open seed-bearing organs in combination with distinct air sacs on pollen, the typical feature of anemophilous plants (Remy 1953; Naugolnykh & Kerp 1996). In many younger taxa belonging to the family Angaropeltidaceae, however, the female reproductive organs became partially or almost completely enclosed, and the air sacs on their pollen grains were less distinct (quasisaccate or protomonosaccate pollen of the *Vesicaspora* type sensu Meyen (1984)). Finally, the air sacs are completely lost (pollen of the *Vittatina* type sensu Meyen (1984)) in some late Permian members of the family Peltaspermaceae.

Nevertheless, our suggestion on the insect pollination of peltasperms remains hypothetic, and it should be tested by new evidences. Indeed, the peltasperms show one of the most ancient events of co-evolution between higher plants and insects (Naugolnykh 2008b) and their interactions were apparently even more complex than it is commonly considered. We can conclude that the trend of seed-bearing organ specialization from open discs to enclosed capsules displays the last phases of pteridosperm s.l. evolution during Palaeozoic/Mesozoic transition. The female reproductive organs of the pteridosperms became more and more specialized, which lead to the formation of closed ovuliferous carpel-like structures, similar to those of the most primitive preangiospermous plants.

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