Permotheca with in situ pollen grains from the Lower Permian of the Urals

VALENTIN A. KRASSILOV¹, SERGEY A. AFONIN¹ AND SERGEY V. NAUGOLNYKH²

¹Palaeontological Institute, 123 Profsoyusnaya, Moscow 117647, Russia. ²Geological Institute, Pyzhevskiy 7, Moscow 109017, Russia.

(Received 4 February 1999; revised version accepted 4 August 1999)

ABSTRACT


Sporangial heads of the pollen organ Permotheca from the Lower Permian of Tschekarda, the Urals, are described as semisyngangiate, with sporangia proximally connate for about one-third to half their length. The sporangial walls are three-layered and vascularized. The pollen grains, studied with LM, SEM and TEM, are transitional protomonosaccate-bilobed to protobisaccate, sulcate, with alveolar infrastructure, lamellate nexine and a tryphine-like surface layer. Chitrid zoosporangia occur in the pollen grains. The similarity to Idanothekion in the sporangial and pollen morphology may indicate phylogenetic relationships.

Key-words—Pteridosperms, sporangia, pollen morphology, phylogeny, Permian.

INTRODUCTION

A puzzling problem in the Permian palynology is a close similarity between contemporaneous palynofloras of different palaeofloristic realms, such as the Angarian, Subangarian, Cathaysian and Gondwana provinces, having widely diverging macrofossil assemblages. Either there were more common elements than suspected on macrofossil evidence or the pollen similarities were due to parallel evolution of phylogenetically unrelated gymnosperm lineages. This problem can be settled only by a comparative analysis of both in situ and dispersed pollen grains and their producing organs. However, few pollen grains are found in situ and still fewer provide a sufficient morphological information.

The gymnosperm pollen organs studied by Russian palaeobotanists, mostly came from the Permian of Subangarian Province including the Urals and the Volga Basin. These areas were ecotonal between the temperate Angarian and tropical Cathaysian realms, supporting a highly diverse gymno-
sperm flora (Meyen, 1984). Pollen-producing organs are relatively common in the rich Subangarian localities, but the data on in situ pollen grains are as yet fragmentary.

In this paper we report on in situ pollen grains of *Permotheca*, a widespread morphotype of sporangial clusters, coming from the Lower Permian Tchekarda locality of fossil plants and insects. Two widely different pollen morphotypes, *Vesicaspora* and *Vittatina* were previously reported from *Permotheca* (Gomankov & Meyen, 1986; Meyen, 1984), a situation that requires a thorough revision.

**MATERIAL AND METHOD**

The Tchekarda locality has been known since 1920s (Martynov, 1928). It is an outcrop of a sandstone, shale and marl sequence in the historical stratotype area of the Kungurian Stage of the Permian System on the Sylva River in the southeastern part of the Ufa-Solikamsk Basin, Central Urals (Ponomareva et al., 1998). The fossil plant assemblage is typical of the Bardian flora that was dominated by conifers and callipterids (Zalessky, 1929, 1937; Meyen, 1984). These deposits also contain a marine fauna of foraminifera, bryozoans, brachiopods and cephalopods.

The following description is based primarily on a single sporangial head from palaeontological collection deposited in the Palaeontological Museum, Moscow. Several synangia figured from the same fossil plant bed by Naugolnykh (1998) and deposited in the Geological Institute, Moscow were studied for additional morphological details.

The sporangial head is preserved as a coaly compression spread in the bedding plane. It was photographed with stereomicroscope CITOVAL-2 and mounted for SEM. The microphotographs of sporangial wall structures and in situ pollen grains were obtained with the CAMSCAN scanning electron microscope. Parts of the pollen masses were extracted from sporangia, macerated in Schultze mixture and individual grains were studied with the light microscope AXIPLAN-2, CAMSCAN and transmission electron microscope JEM-100B-1 (JEOL). Pollen grains selected for TEM were fixed in OsO₄ (1%) for two hours, sectioned using an ultratome LKB-3 and then stained with Reynolds lead and uranil acetate.

**SYSTEMATICS**

*Genus—PERMOTHECA* Zalessky

**PERMOTHECA DISPARIS** (Zalessky) Naugolnykh

Pl. 1, figs 1-6; Pl. 2, figs 1-12

*Permotheca disparis* Naugolnykh 1998; p. 96, fig. 55.

*Description*—The sporangial head in PI. 1, fig. 1 shows six sporangia radially spreading in the bedding plane, with a central scar of a stalk. The sporangia are preserved as compressions split in the median plane and partly encrusted with calcium carbonate, proximally appressed, distally diverging. As seen with SEM, the sporangial locules are proximally separated by thick common walls extending one-third to half their length (Pl. 1, fig. 3). There is no evidence of a cushion or pad of basal tissue.

The individual sporangia are obovate-elliptical, up to 4 mm long, with a maximum width 1.4-2 mm above the middle, gradually tapering to the base and more abruptly to the apex which is bluntly pointed. Their inner face is traversed by a median ridge marking the line of dehiscence. At low magnification the sporangial walls show either longitudinal or slightly oblique to midline or else transverse striation. As seen with SEM, the striation marks the cell files of epidermis and inner layers (Pl. 1, figs 3, 4).

The epidermal cells are narrow, fusiform, of uniform width (about 40 μm), arranged in the gently arched axial files. There is at least a single subepidermal layer of slightly broader fusiform cells and the inner layer of transverse interfingered wedge-shaped cells. The latter appear shrivelled, forming broken files with occasional twisted or protruding cells. The vascular bundles occur in the middle layer of the sporangial walls (protruding in the locule when the inner layer is not preserved) extending along the borders of fused sporangia and diverging at their separation. They consist of long fusiform tracheids (about 30-40 μm), with short to long oblique end walls (Pl. 1, fig. 6), spirally thickened with tight coils wider than their intervening spaces (Pl. 1, fig. 5), 5-7.5 μm broad, occasionally anastomosing.

Masses of pollen grains occur in the locule, sometimes directly on the vascular layer where the inner layer is resorbed. Sixty pollen grains were separated from the pollen masses showing variation in shapes and dimensions. The equatorial midplane outline is elliptical, long axis 50-85 (mean 68) μm, short axis 30-56 (mean 45) μm, broadly rounded over the ends of the long axis, flattened or slightly constricted over the ends of the short axis. The body is transversely elliptical or nearly circular, laterally fringed by a narrow strip of the saccus sexine typically about 3 μm wide, occasionally slightly interrupted, proximally embraced by the arcuate saccus roots for about one-fifth its width on both sides, with the sexine of the saccus gradually attenuating over the cappa margins (Pl. 2, figs 7-10). The distal face shows the saccus exine converging over the body or leaving an elongate cappula typically about 6-10 μm wide, traversed by a narrow slit (Pl. 2, fig. 8). In lateral view the body is trapezoid ("keystone-shaped"), with the cappa smoothly arched, the cappula flat, incised in the middle (Pl. 2, fig. 11). The saccus lobes form wedge-shaped extensions over the body meeting at the midline.

The cappa and sacci are psilate, with exterior brochi sometimes marked on the outside as polygonal depressions.
1. *Permotheca disparis*, compressed sporangial head, Palaeontological Institute, Specimen No. 4748/15, x 9. Other photographs, except fig. 2, are from this specimen.

2. Impression of a similar head from the same locality, Geological Institute, Specimen No. 3737/202, x 4.

3. Sporangia showing longitudinal files of epidermal cells and transverse files lining the locule, SEM, x 55.

4. Base of the sporangial head showing proximal fusion of sporangia, SEM, x 37.

5. Distal view of a pollen grain attached to a tracheid, showing the cappula, SEM, x 950.

6. Tracheids of the sporangial vascular bundles, SEM, x 393.

The cappula is scabrate or irregularly micro verrucate. The roots of the sacci are delimited by thick ridges. Split grains show a prototessate infrastructure of thick endosereal elements arising from the corpus and traceable halfway to the outer wall, distally branching repeatedly to form a three-dimensional pattern of elongate brochi (Pl. 2, fig. 4), polygonal in surface view. The exterior brochi are up to 4 μm wide.

The sporoderm thin sections show a thick tectum underlain by an alveolate infrastructure with large irregular lumina basally supported by a continuous foot-layer. The innermost layer is electronically denser, 0.12 μm thick, with 6-7 distinct lamellae, each 0.02 μm thick. The sporoderm of cappa is 0.9 μm thick. The distal sporoderm is thinner, with the alveolate infrastructure reduced over the cappula, lacking in the sulcus. In some sections, a layer of small dense bodies covered by a thin membrane, supposedly a tryphine-like material of tapetal origin, is discernible above the tectum (Pl. 2, fig. 12). At the root of the saccus the sporoderm is invaginated inside the body (Text-figure 1).

Some pollen grains contain sporangia of chitrid fungi
preserved as spheroidal, slightly angular bodies about 8-16 μm in diameter (Pl. 2, figs 7, 8).

**DISCUSSION**

The genus *Permotheca* was based on a few radial sporangial heads from the Kazanian (mid-Permian) deposits of Tatarstan briefly described as *Permotheca sardykensis* (Zalessky, 1929). Similar material from the Kungurian of the Urals was assigned by the same author to *Asterodiscus disparis* (Zalessky, 1937). The latter material was revised by Naugolnykh who first published it, together with ovulate disks, under the name *Peltaspermum retensorium* (Naugolnykh & Kerp, 1996), later transferred to *Permotheca disparis* (Naugolnykh, 1998). He also found loose strobili of many spirally attached *Permotheca*-type heads. These finds were used to reconstruct the strobilus shown in Text-figure 2.

Since the dimensions and the number of sporangia vary along the axis, these characters are of a little taxonomic significance. The species of *Permotheca* based on external morphology of dispersed heads alone may well belong in a single species. However, their *in situ* pollen grains were assigned to different morphotypes (Gomankov & Meyen, 1986).

In its strobilate aspect with sporangial heads arranged in a single spiral series *Permotheca* stands apart from pteridospermous pollen organs with sporangia or synangia born in three-dimensional or planate branching systems or else on laminar pinnules (Millay & Taylor, 1979). A taxonomic demarcation of dispersed sporangia remains a problem because radial sporangial clusters or synangia are known in a number of Palaeozoic taxa, such as *Zimmemannitheca*, *Aulacotheca*, *Crossotheca*, *Feraxotheca*, *Callandrium*, *Idanothekion*, as well as the Mesozoic *Pteruchus*, *Pteroma*, *Harrisithecium*, *Meeusella* and their allied forms (Millay & Eggert, 1970; Millay & Taylor, 1979; Stidd & Hall, 1970; Harris, 1964; Townrow, 1965; Retallack, 1983; Taylor *et al.*, 1984; Krassilov & Bugdaeva, 1988a, b). In these genera, however, the sporangia are either free, as in the Lower Carboniferous *Zimmemannitheca*, or, if synangiate or semisynangiate, have a basal cushion of parenchymous tissue that is apparently lacking in *Permotheca*. Other distinctive features are vascularization and the degree of sporangial fusion in the semisynangial structures. Vascularization of sporangia is shared by *Permotheca* with *Telangium* and *Idanothekion*, but in these

---

**PLATE 2**

1. Sporoderm ultrastructure of cappa showing tectum, alveolate infra-structure, and nexine. TEM, x 12,000.
2. Close-up of the same section showing the sexine/flame-like nexine boundary (arrow), TEM, x 40,000.
3. Sulcus area with attenuate alveolar infrastructure and lamellated nexine, TEM, x 12,000.
4. Split grain showing protosaccate structure, SEM, x 2833.
5. Pollen grain, proximal aspect, SEM, x 900.
6. Pollen grain, latero-distal aspect, SEM, x 1150.
7. Two pollen grains with a clearly defined sulcus and the saccus sexine overlapping the cappula; right grain with fungal zoosporangium, LM, x 720.
8. Pollen grain with a fungal zoosporangium, LM, x 720.
9, 10. Pollen grains showing saccus sexine overlapping the cappula, with narrow lateral connections interrupted on one side, LM, x 720.
11. Same pollen grain as in fig. 6, with trapezoid body in proximo-lateral view with the sacci nearly converging over the cappula; note micropunctate infrastructure of the cappa, LM, x 720.
12. Orbicule-like bodies and the tryphine-like membrane over the tectum, TEM, x 5,000.
Carboniferous genera the sporangia are fused for about two-thirds or even four-fifths of their length and the vascular bundle extends in the median plane. Individual sporangia are rather similar to Arberiella in general shape and epidermal structure (as shown in Pant & Bhatnagar, 1972; Zavada, 1991) but in the latter genus sporangia are stalked and are arranged in either branching or discoid structures (Rigby & Chandra, 1990).

Notably, in Permotheca and other Palaeozoic sporangia, the wall remains multilayered even after shedding of the pollen grains, whereas in the Mesozoic sporangia the inner wall layers are typically resorbed at maturity and the ripe pollen grains are covered only with an epidermal layer. This evolutionary change apparently relates to a more efficient use of sporangial tissues as a trophic resource for developing pollen grains.

Remarks on the pollen grains—The pollen grains are apparently of the same type as found in situ in the Upper Permian Permotheca vesicasporoides (Meyen, 1984; Gomankov & Meyen, 1986). The latter were described with LM as monosaccate, comparable with Vesicaspora Shemel emend. Wilson & Venkatatehala (1963) and with the pollen grains of Idanothekion glandulosum Millay & Eggert (1970) assigned to the same morphotype. However, Balme (1995) suggested Falcisporites Leschik emend. Klaus, rather than Vesicaspora, as a more appropriate pollen-genus for the in situ pollen grains of Permotheca vesicasporoides. He assigned to Falcisporites also the in situ pollen grains of Pteruchus africanus Thomas that are externally quite similar to those of Permotheca. Falcisporites belongs to a group of the Late Permian to Mesozoic pollen morphotypes including also Pityosporites Seward emend. Manum, Alisporites Daugherty emend. Nilsson, Klausipollenites Jansonius, and some other less frequently used pollen-genera. They allegedly differ in the relative development of sulcus (typically present, elongate-rectangular in Falcisporites, but less conspicuous in Alisporites and apparently lacking in Klausipollenites, see Clarke, 1965; Scheuring, 1970; Jansonius, 1971; Foster, 1979) and the lateral connection of sacci (typically present in Klausipollenites, but less conspicuous in Alisporites and apparently lacking in Klausipollenites, see Clarke, 1965; Jansonius, 1971). However, these characters vary with developmental stage and preservation. In transitional forms, such as Vesicaspora or Klausipollenites, a demarcation of bisaccate pollen grains from monosaccate with strongly bilobed saccus is often arbitrary (Jizba, 1962; Clarke, 1965; Lindström et al., 1997). In the in situ grains of Permotheca both monosaccate-bilobed and bisaccate conditions are met in a single sporangium.

A more profound distinction might have been provided at the ultrastructural level by infrastructure which is alveolar in Vesicaspora, but granular in Pteruchus africanus and supposedly in the allied dispersed morphotypes. Since the pollen grains of Permotheca have an alveolar infrastructure they seem closer to Vesicaspora, though differing from the latter in a better defined corpus and a more constantly developed sulcus. Haptotypic marks are lacking in our material, as well
in the Late Pennsylvanian Vesicaspora, though sometimes present in the mid-Pennsylvanian representatives of the genus (Millay & Taylor, 1974).

A thin membrane over the tectum is also a feature observed in some Carboniferous seed-fern pollen grains. The membrane was conventionally described as tapetal (Taylor & Taylor, 1987). It is actually comparable to trypnine of angiosperm pollen grains where it is a surface deposit of tapetal origin.

On evidence of both sporangial and pollen grain morphology, Permotheca seems most closely related to the Carboniferous callistophytes.

Acknowledgements: This work was supported by the Russian Foundation of Basic Research, Grant 98-04-49010.

REFERENCES


