

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

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ABSTRACT

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Sporangial heads of the pollen organ *Permotheca* from the Lower Permian of Tschekarda, the Urals, are described as semisynangiate, 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.

सारांश

यूराल के अधो परमियन युग के परमोथीका में स्थित स्वस्थाने परागकण

वैलेन्टीन ए. क्रासीलोव, सर्गेई ए. एफोनिन एवं सर्गेई वी. नाउगोलिन्ख

यूराल की शेकरदा संस्थिति से प्राप्त अधोपरमियनयुगीन पराग अंग परमोथीका के स्पोरैन्जियल शीर्ष अर्धसंधानी रूप में वर्णित किये गए हैं, जिनका स्पोरैन्जिया निकटस्थ कोणीय है तथा अपनी लम्बाई की तुलना में एक तिहाई से आधे के बीच है। स्पोरैन्जियल भित्तियाँ त्रिस्तरीय तथा संवहनी हैं। परागकणों का सरल सूक्ष्मदर्शी, क्रमवीक्षण इलेक्ट्रॉन सूक्ष्मदर्शी तथा संचारित इलेक्ट्रॉन सूक्ष्मदर्शी द्वारा अध्ययन करने पर ये कूपिका की अवसंरचना, पटलिकीय नेक्ससइन एवं ट्रिफाइन की भाँति पृष्ठ सतह के साथ संक्रमित आय एकसकोशीय द्विपालिक से आय द्विसकोशीय सल्कस युक्त प्रदर्शित हुए हैं। परागकणों में काइट्रिड चलबीजाणुधानिक भी प्राप्त हुए हैं। स्पोरैन्जियल तथा पराग आकारिकी में *इडेनोथेकियोन* से इनकी समरूपता जातिवृत्तीय सम्बन्धों का संकेत कर सकती है।

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 prob-

lem 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 southern 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 AXIOPLAN-2, CAMSCAN and transmission electron microscope JEM-100B-1 (JEOL). Pollen grains selected for TEM were fixed in OsO_4 (1%) for two hours, sectioned using an ultratome LKB-3 and then stained with Reynolds lead and uranyl 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 Pl. 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 interfingering 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. 7). 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 sacchi are psilate, with exterior brochi sometimes marked on the outside as polygonal depressions.

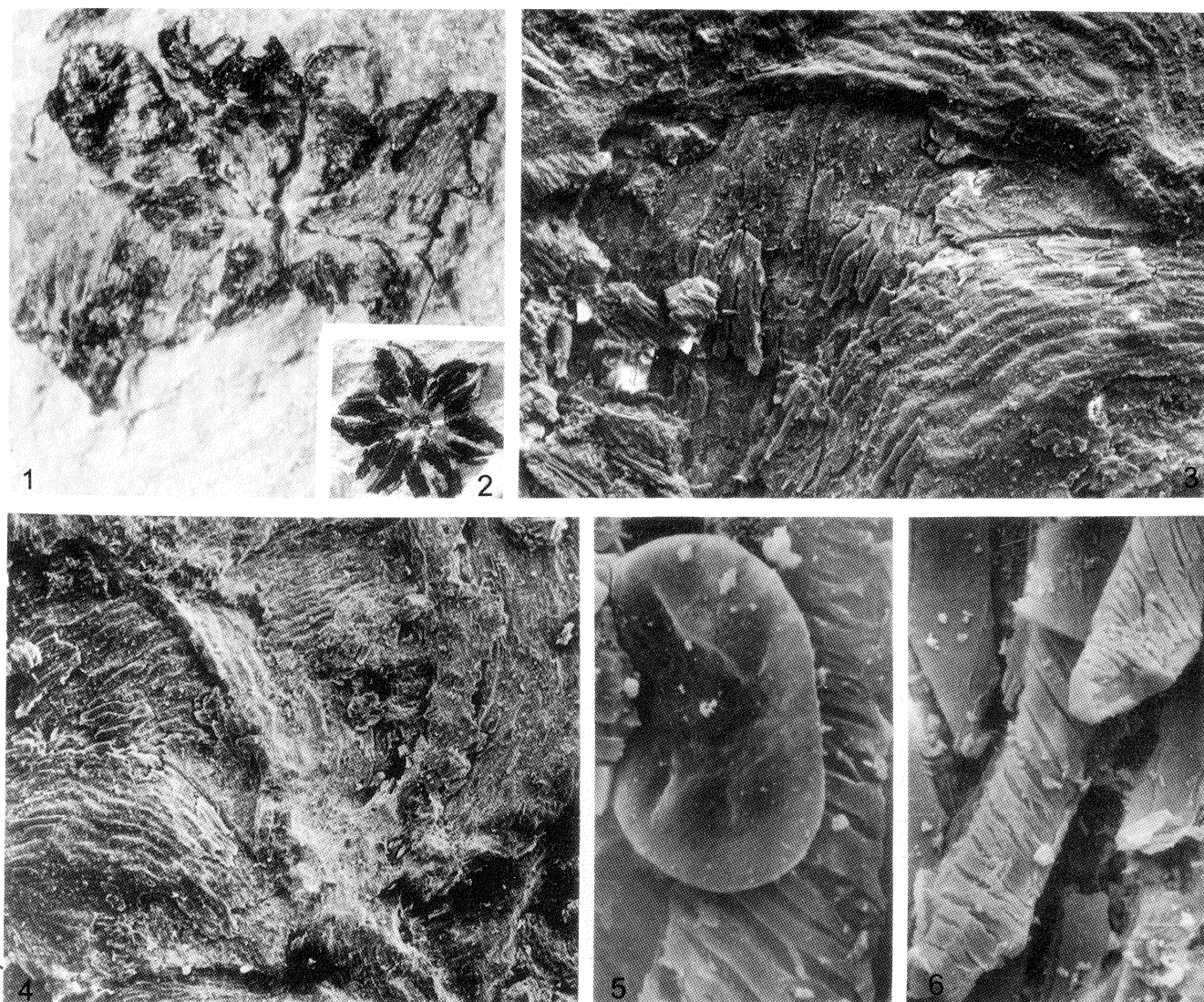


PLATE 1

1. *Permothecca 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

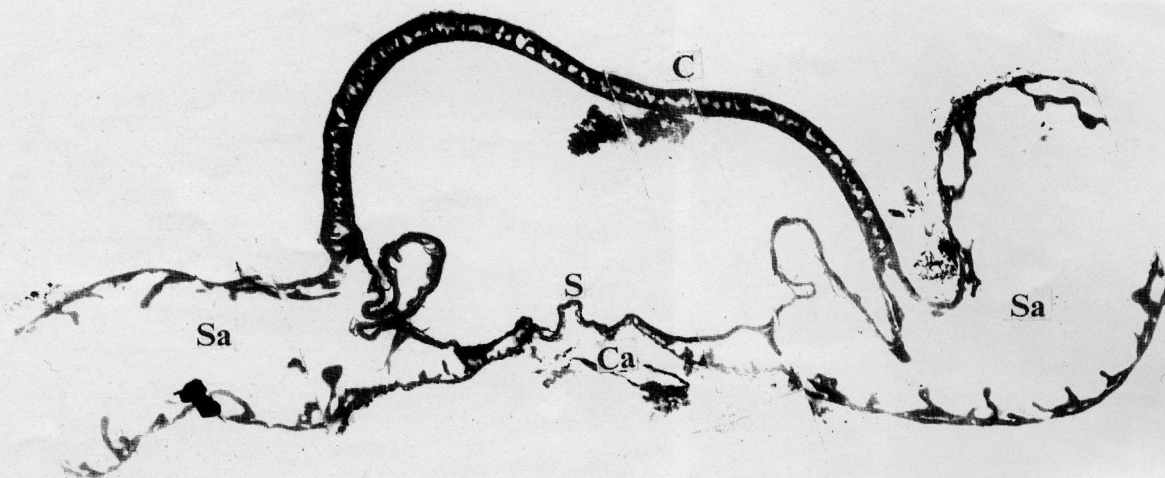
- files lining the locule, SEM, x 55.
4. Base of the sporangial head showing proximal fusion of sporangia, SEM, x 37.
5. Distal view of a pollen grain attached to a tracheid, showing the cappula, SEM, x 950.
6. Tracheids of the sporangial vascular bundles, SEM, x 393.

The cappula is scabrate or irregularly microverrucate. The roots of the sacci are delimited by thick ridges. Split grains show a protosaccate infrastructure of thick endosexinal 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



Text-figure 1—Section of entire pollen grain showing a thick sporoderm of the cappa (C), a thinner sporoderm of the cappula (Ca), sulcus (S) and infolded nexine at the saccus (Sa) roots. TEM, 4,000.

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 sardyensis* (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.

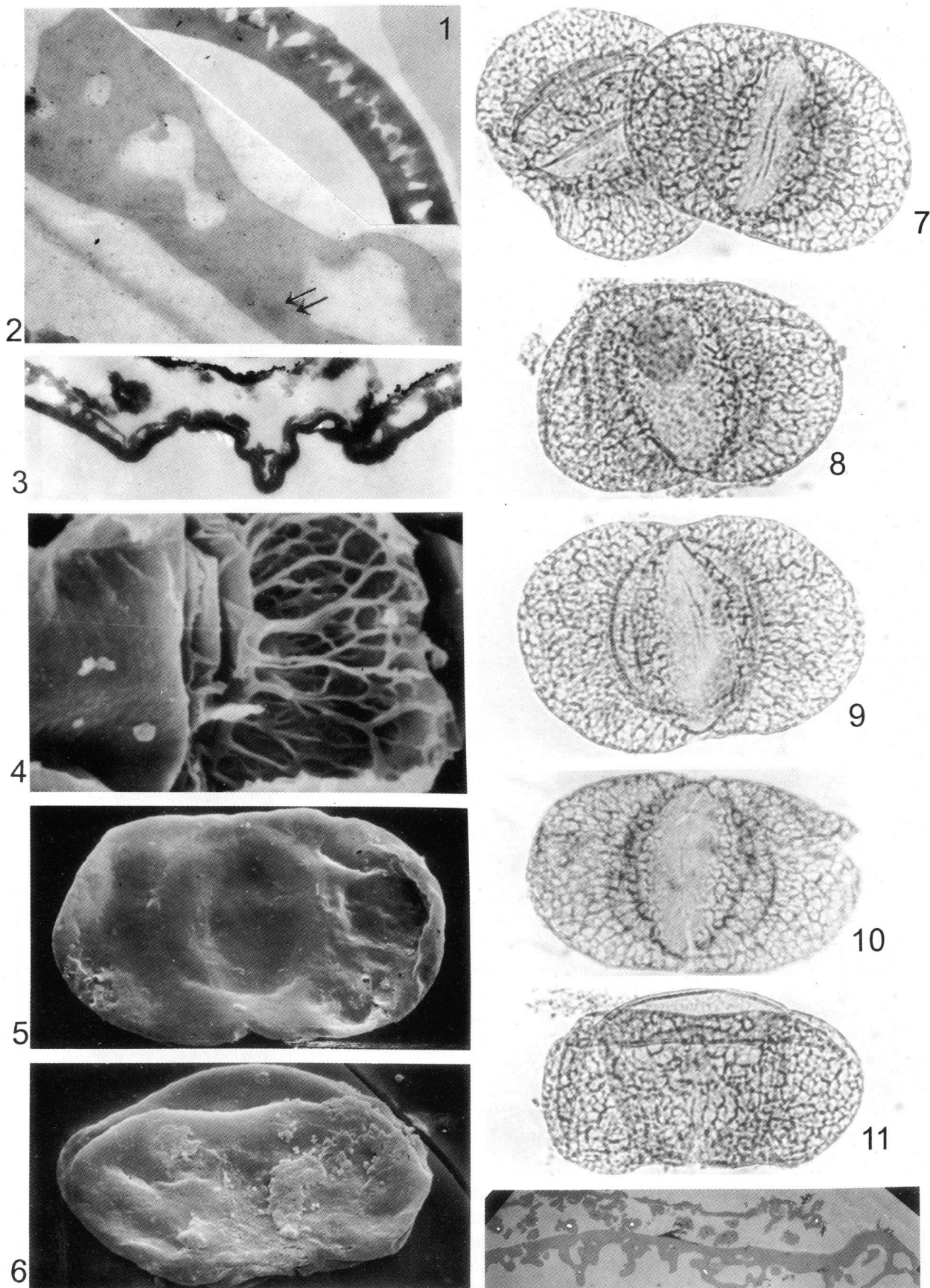
Since the dimensions and the number of sporangia vary along the axis, these characters are of a little taxonomic significance. The species of *Permotheca* based on external morphology of dispersed heads alone may well belong in a single species. However, their *in situ* pollen grains were assigned to

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 *Zimmernannitheca*, *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 *Zimmernannitheca*, 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/lamellate nexine boundary (arrow), TEM, x 40,000.
3. Sulcus area with attenuate alveolar infra-structure 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 cappa, 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 sacchi nearly converging over the cappula; note micropunctate infra-structure of the cappa, LM, x 720.
12. Orbicule-like bodies and the tryphine-like membrane over the tectum, TEM, x 5,000.

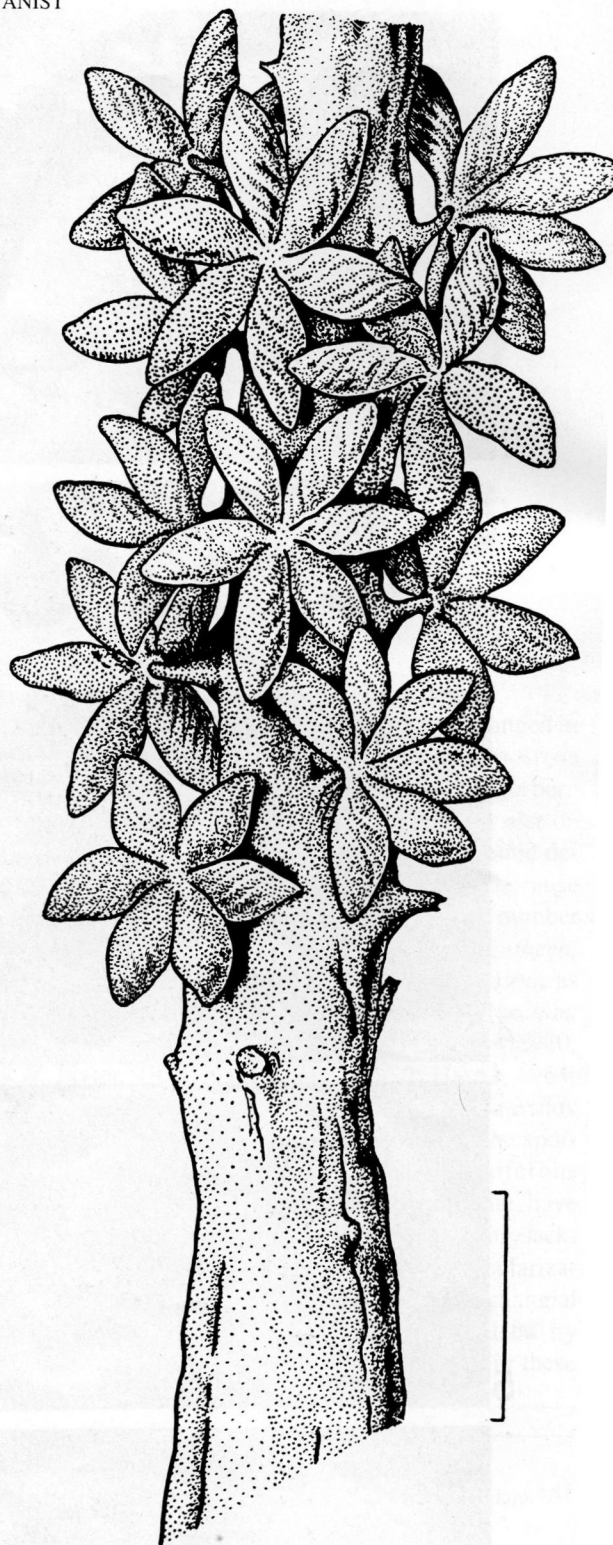


Carboniferous genera the sporangia are fused for about two-thirds or even four-fifths of their length and the vascular bundle extends in the median plane. Individual sporangia are rather similar to *Arberiella* in general shape and epidermal structure (as shown in Pant & Bhatnagar, 1972; Zavada, 1991) 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 & Venkatachala (1963) and with the pollen grains of *Idanotekion 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 *Falcisporites*, 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



Text-figure 2—Reconstruction of strobilus with *Permotheca*-type sporang heads, scale bar 1 cm.

closer to *Vesicaspora*, though differing from the latter in a better defined corpus and a more constantly developed sulcus. Haplotypic 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 tryphine of angiosperm pollen grains where it is a surface deposit of tapetal origin.

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

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