Chapter 14

IN SITU POLLEN AND SPORES IN PLANT EVOLUTION

14C – THE IMPORTANCE OF IN SITU POLLEN AND SPORES IN UNDERSTANDING THE BIOLOGY AND EVOLUTION OF FOSSIL PLANTS

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INTRODUCTION

There are two major approaches to the study of fossil pollen grains and spores. In one, the principal thrust of the research is aimed at the utilization of pollen and spores as biostratigraphic markers (Volkheimer & Zavattieri 1991) or as indicators of past floras. Studies of this type rely on grains, dispersed (*sporae dispersae*) in the sediment, which are subsequently macerated from the rock matrix. Historically, *sporae dispersae* were examined relative to a variety of biological parameters ranging from aperture organization to the nature and significance of wall layers. In many of these studies little or nothing was known about the plants that produced the grains, although in some instances taxonomic affinities were inferred from either the overall grain morphology or the sporoderm ultrastructure (Kurmann & Taylor 1987; Zavada & Dilcher 1988), while in other instances additional features such as the aperture and nature of the ornament were documented (Doyle *et al*. 1982; Ward *et al*. 1989).

The second approach is directed at the examination of pollen grains and spores in a more biological context. As an extensive data base of plant megafossil reproductive organs was assembled for Carboniferous plants, especially those preserved as calcitic permineralizations termed coal balls, an increasing number of studies were concerned with the pollen grains and spores preserved in these fertile organs (Taylor & Taylor 1987; Osborn 1991). With greater access to scanning electron microscopy, and the increased use of transmission electron microscopy, the investigation of fossil grains preserved in situ has provided a wealth of data concerning the biology of these fossil organisms. For example, information ranging from microsporogenesis (Taylor 1990) to the functional aspects of pollen and spore walls (Taylor & Zavada 1986) has been documented.

The intent of this paper is to review the type of information that can be obtained from the study of in situ pollen and spores. We have concentrated principally on Paleozoic specimens, although a few Mesozoic examples are cited, and we have attempted to include as many major groups of plants as possible. Although numerous excellent studies have examined in situ fossil pollen and spores with only transmitted light, we have selected examples in which transmission and scanning electron microscopy have played important roles in elucidating significant biological questions. It is beyond the scope of this paper to cover all potential avenues of investigation relating to the study of in situ grains, nor is it possible to treat all groups for which data are currently available. Rather, we discuss in situ grains as they relate to the following broad categories: haptotypic marks, saccus development, sporoderm development, tapetal membranes and orbicules, enigmatic fossils, taxonomic variation, phylogenetic considerations, and terminology and techniques. Table 1 provides only a partial listing of the major groups of Paleozoic and Mesozoic plants for which information is currently available about in situ pollen and spores. The spores of early land plants are discussed by Edwards & Richardson in this volume (Ch. 14A), and Friis & Pedersen detail studies of in situ angiosperm pollen (Ch. 14B).

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HAPTOTYPIC MARKS

A great deal of information exists about the development of fossil pollen grains and spores, including stages in microsporogenesis (Taylor 1990). To examine developmental changes, fossil pollen and spores are typically macerated from a single sporangium (Pl. 1, Fig. 1), or where there is synchronous development, from several sporangia (Pl. 1, Fig. 2). Depending on the nature of the study, information is then extrapolated between stages, much as is done in developmental investigations of extant pollen and spores.

In the monosaccate cordaitean pollen grain *Felixipollenites* (Pl. 1, Fig. 5), produced by the pollen organ *Gothania*, grains range up to 180 µm in diameter (Taylor & Daghlian 1980). Specimens macerated from the same pollen sac may show either radial or bilateral symmetry, and have highly variable haptotypic marks. These may range from distinctly monolete to trilete, with up to 70% having intermediate forms. Interestingly, regardless of the geometry of the mark, the ultrastructure of the suture is uniform, consisting of a low ridge supported by a series of small plates aligned at right angles to the suture (Taylor & Daghlian 1980). In *Felixipollenites*, and other grains with variable haptotypic marks (Schopf 1948), it is difficult to determine whether this difference is the result of meiotic abnormality, grain crowding within the sporangium, or the abortion of some pollen grains. Despite the inability to determine why these in situ grains are so variable, the importance ascribed to the aperture in pollen and spore taxonomy would likely result in the establishment of several taxa if these grains were encountered in *sporae dispersae* assemblages.

TABLE 1. Selected taxa for which ultrastructural information is known about the pollen/spores, excluding angiosperms. Letter in brackets denotes geologic age (C=Cretaceous; D=Devonian; E=Eocene; J=Jurassic; L/R=Liasso-Rhaetic; M=Miocene; P=Pennsylvanian; Perm.=Permian; Plio.=Pliocene; T=Triassic). These taxa have not been included in the "List of taxa". Authors of these names can be found in the references cited in parentheses after each name.

LYCOPHYTA
- *Lepidocarpon takhtajanii* [P] (Taylor 1974)
- *Achlamydocarpon belgicum* [P] (Taylor 1974; Taylor & Brack-Hanes 1976a)
- *A. varium* [P] (Taylor & Brack-Hanes 1976b)
- *Endosporites* sp. [P] (Brack & Taylor 1972)
- *Valvisisporites auritus* [P] (Gastaldo 1981)
- *Selaginellites crassicinctus* [P] (Taylor & Taylor 1990)
- *Erlansonisporites sparassis* [C] (Taylor & Taylor 1988)
- *Horstisporites iridodeus* [C] (Taylor & Taylor 1988)
- *H. semireticulatus* [J] (Kempf 1971)
- *Bacutriletes triangulatus* [C] (Taylor & Taylor 1988)
- *Hughesisporites patagonicus* [C] (Taylor & Taylor 1988)
- *Paxillitriletes menendezii* [C] (Baldoni & Taylor 1985)
- *P. vittatus* [C] (Kovach & Dilcher 1985)

Incertae sedis (lycopod affinities probable)
- *Nikitinsporites canadensis* [D] (Taylor *et al.* 1980)
- *Barinophyton citrulliforme* [D] (Taylor & Brauer 1983)
- *Protobarinophyton pennsylvanicum* [D] (Cichan *et al.* 1984)
- *Cabochonicus carbunculus* [T-C] (Batten & Ferguson 1987)
- *Setosisporites hirsutus* [P] (Kempf 1973)
- *S. brevispinosus* [P] (Kempf 1973)
- *Banksisporites pinquis* [T] (Kempf 1971)
- *Nathorstisporites hopliticus* [J] (Kempf 1971)
- *Margaritatisporites turbanaeformis* [J] (Kempf 1971)
- *Istisporites murrayi* [J] (Kempf 1971)

SPHENOPHYTA
- *Bowmanites dawsonii* [P] (Taylor 1970; Taylor 1986)
- *Sphenostrobus iowensis* [P] (Taylor 1986)
- *Peltastrobus reediae* [P] (Taylor 1986)
- *Sentistrobus goodii* [P] (Taylor 1986)
- *Elaterites triferens* [P] (Kurmann & Taylor 1984a)
- *Calamostachys germanica* [P] (Brousmiche & Lugardon 1990)
- *Palaeostachya feistmantelii* [P] (Brousmiche & Lugardon 1990)

PTERIDOPHYTA
Marattiales
- *Scolecopteris fragilis* [P] (Millay & Taylor 1984)
- *S. latifolia* [P] (Millay & Taylor 1984)
- *S. mamayi* [P] (Millay & Taylor 1984)
- *S. monothrix* [P] (Millay & Taylor 1984)
- *S. nigra* [P] (Millay & Taylor 1984)
- *S. parvifolia* [P] (Millay & Taylor 1984)
- *S. saharaensis* [P] (Millay & Taylor 1984)
- *S. vallumii* [P] (Millay & Taylor 1984)

Filicales
- Botryopteridaceae
  - *Botryopteris* sp. [P] (Millay & Taylor 1982)
  - *B. globosa* [P] (Millay & Taylor 1982)
  - *B. forensis* [P] (Millay & Taylor 1982)
  - *B. cratis* [P] (Millay & Taylor 1982)
- Gleicheniaceae
  - *Szea sinensis* [Perm.] (Yao & Taylor 1988)
- Cyatheaceae
  - *Cyatheacidites tectifera* [C] (Kurmann & Taylor 1987)
- Dicksoniaceae
  - *Onychiopsis psilotoides* [C] (Friis & Pedersen 1990)

Salviniales
- *Azolla nana* [M] (Kempf 1969)
- *A.* cf. *aspera* [Plio.] (Kempf 1969)
- *Salvinia cerebrata* [M] (Kempf 1973)

Zygopteridales
- *Biscalitheca musata* [P] (Taylor & Millay 1977a)

Incertae sedis
- *Cyathotheca tectata* [P] (Taylor 1972)

PROGYMNOSPERMOPHYTA
Archaeopteridales
- *Archaeopteris* cf. *jacksonii* [D] (Pettitt 1966)

PTERIDOSPERMOPHYTA
Lyginopteridales
- *Crossotheca* sp. [P] (Millay *et al.* 1978)
- *Potoniea illinoiensis* [P] (Stidd 1978; Taylor 1982)
- *P. carpentieri* [P] (Taylor 1982)
- *Schopfiangium varijugatum* [P] (Stidd *et al.* 1985)
- *Phacelotheca pilosa* [P] (Meyer-Berthaud & Galtier 1986)

Medullosales [all *Schopfipollenites* except: *Parasporotheca* (*Parasporites*)]
- *Halletheca reticulata* [P] (Taylor 1978)
- *Bernaultia sclerotica* [P] (Taylor & Rothwell 1982)
- *B. formosa* [P] (Taylor 1978)
- *Dolerotheca* sp. [P] (Taylor 1978)
- *Sullitheca dactylifera* [P] (Taylor 1982)
- *Rhetinotheca tetrasolenata* [P] (Taylor 1978)
- *R. patens* [P] (Taylor 1982)
- *Boulayatheca fertilis* [P] (Kurmann & Taylor 1984b)
- *Schopfitheca boulayoides* [P] (Taylor 1978)
- *Aulacotheca iowensis* [P] (Taylor 1976a, b, 1978)
- *Codonotheca caduca* [P] (Taylor 1976a,b, 1978)
- *Parasporotheca leismanii* [P] (Millay *et al.* 1978; Taylor 1982)

Callistophytales
- *Idanothekion callistophytoides* [P] (Millay & Taylor 1974, 1976)

Glossopteridales
- *Arberiella* sp. (*Protohaploxypinus*-type and *Striatopodocarpites*-type) [Perm.] (Zavada 1991)

Corystospermales
- *Pteruchus dubius* [*Pteruchipollenites* or *Alisporites*] [T] (Taylor *et al.* 1984; Zavada & Crepet 1985; Osborn 1991)
- *P. africanus* [T] (Zavada & Crepet 1985)
- *P. papillatus* [T] (Zavada & Crepet 1985)

Caytoniales
- *Caytonanthus arberi* [J] (Pedersen & Friis 1986; Zavada & Crepet 1986; Osborn 1991)
- C. *kockii* [J] (Pedersen & Friis 1986)

CONIFEROPHYTA
Cordaitales
- *Cordaianthus* sp. [*Florinites*] [P] (Millay & Taylor 1974, 1976)
- *Cordaianthus* sp. [*Sullisaccites*] [P] (Millay & Taylor 1974, 1976)
- *Gothania lesliana* [*Felixipollenites*] [P] (Millay & Taylor 1974, 1976; Taylor & Daghlian 1980)

Coniferales
- Cheirolepidiaceae (all *Classopollis*-type grains)
  - *Classostrobus comptonensis* [C] (Taylor & Alvin 1984)
  - *Hirmeriella muensteri* [L/R] (Pettitt & Chaloner 1964)
  - *Classopollis classoides* [J] (Rowley & Srivastava 1986)
- Podocarpaceae
  - *Millerostrobus vesiculatus* [T] (Taylor, Delevoryas & Hope 1987)
  - *Morenoa fertilis* [C] (Del Fueyo *et al.* 1990)
  - *Rugubivesiculites rugosus* [C] (Zavada & Dilcher 1988)
  - *Squamastrobus tigrensis* [C] (Archangelsky & Del Fueyo 1989)
  - *Trisacocladus tigrensis* [C] (Baldoni & Taylor 1982)

TABLE 1 (continued)

Taxodiaceae
Elatides williamsonii [J] (Kurmann 1991)
Drumhellera kurmanniae [C] (Serbet & Stockey 1991)
Metasequoia milleri [E] (Rothwell & Basinger 1979)

CYCADOPHYTA
Cycadales
Androstrobus balmei [J] (Hill 1990)
Cycadeoidales
Cycadeoidea dacotensis [C] (Taylor 1973; Osborn 1991)
Leguminanthus siliquosus [T] (Ward *et al.* 1989)
Pentoxylales
Sahnia laxiphora [C] (Osborn *et al.* 1991)

GNETOPHYTA
Equisetosporites spp. [C] (Osborn *et al.* 1993)
Ephedripites sp. [C] (Trevisan 1980)

INCERTAE SEDIS
Cyclusphaera psilata [C] (Taylor, Zavada & Archangelsky 1987)
Erdtmanitheca texensis (*Eucommiidites*-type) [C](Pedersen *et al.* 1989)
Erdtmanispermum balticum (*Eucommiidites*-type) [C] (Pedersen *et al.* 1989)
Lasiostrobus polysaccus [P] (Taylor & Millay 1977b)
Melissiotheca longiana [P](Meyer-Berthaud 1986, 1989)
Nanoxanthiopollenites mcmurrayi [P] (Taylor 1980)

PROBLEMATIC FOSSILS
Protosalvinia sp. [D] (Taylor & Taylor 1987b)
Parka decipiens [D] (Hemsley 1989, 1990)

SACCUS DEVELOPMENT

Vesiculate Carboniferous pollen grains similarly provide insight into the organization, development and evolution of the saccus in some groups (Millay & Taylor 1976). For example, in *Florinites* grains macerated from *Cordaianthus concinnus* (Millay & Taylor 1974), saccus attachment occurs on both the proximal and distal poles. Moreover, most of these grains are alete at maturity, although a faint trilete mark may be observed on the proximal surface in a few. In *Felixipollenites* the saccus may also be attached to the corpus on both the proximal and distal surfaces, but as the grains mature and the saccus expands, the attachment becomes only proximal (Pl. 1, Fig. 4; Taylor & Daghlian 1980). This configuration indicates that in these monosaccate grains the saccus did not function harmomegathically because germination was confined to the proximal pole.

In the Carboniferous cordaites and conifers, as well as in pollen of the seed fern *Callistophyton* (i.e. *Vesicaspora*), the inner surface of the corpus is ornamented by delicate, inwardly facing projections termed endoreticulations (Pl. 1, Fig. 3, 4). This condition is sometimes referred to as eusaccate. Stages in the development of the saccus in a large number of pollen grains of this type indicate that endoreticulations result from the separation of sporoderm layers during saccus expansion, much as they do in extant saccate grains (Millay & Taylor 1974; Kurmann 1989).

Saccus organization in monosaccate and bisaccate Carboniferous grains is quite different from the configuration seen in many Permian and Mesozoic vesiculate pollen grains. In the latter, a delicate reticulum of continuous threads extends from the inner wall of the saccus to the outer surface of the corpus (Pl. 1, Fig. 6; Taylor *et al.* 1984; Pedersen & Friis 1986). Although this condition has been termed protosaccate by Scheuring (1976), the fact that it occurs in several distantly related groups of plants suggests that it has little phylogenetic significance. Rather, some of these grains represent different levels of saccus evolution associated with anemophily in widely differing taxa. For example, in the voltzialean grain *Sertostrobus* (Pl. 1, Fig. 6) the protosaccate type of organization may have functioned principally in wind dispersal. In the Carboniferous cordaites and callistophytalean seed ferns, on the other hand, the eusaccus may have attained a level of development in which the primary function was one of harmomegathy in which the sacci were able to close over the distal aperture, and thus reduce desiccation.

In at least one seed fern group (Medullosales), the large (230 μm) pollen of *Parasporites* is characterized by what are regarded as vestigial sacci (Millay *et al.* 1978). In these grains no threads of sporopollenin extend between the saccus and corpus, nor is there any evidence of endoreticulations (Taylor 1982). Perhaps *Parasporites* reflects an evolutionary shift in pollination biology from anemophily to entomophily. Although grains of this type are included within the Medullosales based principally on the alveolate nature of the sexine, the pollen organs are structurally and morphologically quite different from other medullosan pollen organs (Millay & Taylor 1979).

SPORODERM DEVELOPMENT

Within the major groups of fossil gymnosperms there appears to be some uniformity in the infrastructure of the pollen grain wall. Within the seed ferns, sporoderm fine structure is known from representative taxa of all groups, except the Peltaspermales (Table 1).

The pollen of the Lyginopteridales is morphologically uniform and includes predominantly radial, trilete grains. The sporoderm has been characterized by several workers as homogeneous, with a uniform infrastructure consisting of a thin nexine and thick, homogeneous sexine (Taylor 1982). To date, the only exceptions to this are the pollen organs *Schopfiangium* (Stidd *et al.* 1985) and *Phacelotheca* (Meyer-Berthaud & Galtier 1986). In pollen from these organs, suggested as having lyginopterid affinities, the sporoderm is alveolate. Within the lyginopterid group, pollen wall development is known only for *Potoniea carpentieri*. Here, the increase in sporoderm thickness is attributed to the addition of lamellae that form as a result of activities of the protoplast (Pl. 1, Fig. 7). In situ studies indicate that at least some of the outer portion of the pollen grain wall forms by tapetal accretion of sporopolleninous orbicules (Taylor 1982).

Perhaps the best known pollen types of all seed ferns are those of the Medullosales. Pollen of *Schopfipollenites* (=*Monoletes*) is large (140-500 μm), and known to have been produced by several types of reproductive organs (Millay & Taylor 1979). The angular deflection of the proximal monolete

mark is the result of bilateral expansion after the grains were released from a tetrahedral tetrad (Pl. 1, Fig. 4). Two elongate grooves separated by an umbo characterize the distal face. The sporoderm of mature grains consists of a lamellate nexine and an alveolate sexine (Taylor 1978). Pollen wall development has been traced in *Schopfipollenites* grains macerated from *Bernaultia sclerotica* (Taylor & Rothwell 1982). The earliest stage in sporoderm ontogeny is detectable in grains approximately 100 µm long. Here, the sporoderm is approximately 2.0 µm thick and homogeneous, and exhibits no apparent differences between nexine and sexine layers. In more mature grains (Pl. 2, Fig. 2), the wall is 4 µm thick and demonstrates early differentiation of sporoderm layers; at this stage there are lamellae visible in the nexine, whereas the sexine is characterized by small lumina. The alveolate sporoderm infrastructure becomes more conspicuous as the sexine continues to expand via separation and plication of lamellae. In the most mature *Schopfipollenites* grains, the sexine region nearest the nexine is disrupted due to continued separation and expansion of the sporoderm (Pl. 2, Fig. 3, 5). From this study it is known that the alveolate sporoderm organization results from the continued expansion of nexine lamellae. This is in marked contrast to the alveolate organization in modern cycad pollen grains, where sporopollenin deposition takes place on radially aligned tubules in the sexine (Audran 1981). Moreover, the nexine in modern cycad pollen is the last layer to be deposited, whereas in *Schopfipollenites* it appears to be the initial sporoderm component.

In situ pollen from the Mesozoic genus *Caytonanthus* (Caytoniales) has also been examined with the aid of electron microscopy (Krassilov 1977; Pedersen & Friis 1986; Zavada & Crepet 1986; Osborn 1991). These grains are typically small (less than 30 µm), bisaccate and monosulcate. In contrast to pollen of the corystosperms, the nexine and sexine of *Caytonanthus* pollen can be distinguished. Although nexine lamellae have been noted in mature grains that have undergone folding and compaction, Osborn (1991) reported their presence in immature grains. This information suggests that lamellae represent a basic unit of the sporoderm, similar to the exine organization found in some Paleozoic seed fern pollen. Vasanthy *et al.* (1990) suggested that the lamellated endexine (=nexine) may constitute a primitive feature that unites several groups of plants.

The best known developmental study of in situ fossil pollen is of *Classopollis* grains recovered from the cheirolepidaceous conifer *Classostrobus comptonensis*, from Lower Cretaceous Wealden sediments (Taylor & Alvin 1984). The grains are circular and average 36 x 25 µm in diameter. They are characterized by a proximal triradiate suture, and a cryptopore on the distal face. Encircling each grain just below the equator is a thickened band termed the girdle. The sporoderm is complex and highly variable in some planes of section. Taylor & Alvin (1984) recognized a well defined nexine with up to 20 lamellae, each approximately 10 nm in thickness (Pl. 3, Fig. 1). The sexine is organized into four zones. The inner of these consists of coarse, radially arranged, anastomosing elements that support a thin tectum. The third sporoderm component is defined by a series of small spaces formed by the bases of numerous spinules that in turn constitute the ornament of the *Classopollis* grains (Pl. 3, Fig. 2).

The earliest identified stage of wall development of this *Classopollis* pollen type includes an amorphous nexine in which lamellae are indistinct, or if distinct, confined to the outer region of the layer. As development of the sporoderm continued, the inner, radially oriented elements of the sexine became electron dense areas above the nexine. At this ontogenetic stage, nexine lamellae are easily distinguishable. Spinules that are typically poorly defined (Pl. 3, Fig. 5) and associated with electron dense material between them, characterize the next phase in the development of the pollen wall. The final stage of sporoderm maturation involves a tapetal membrane system that contributed sporopollenin to the surface sculpture. The basis for this hypothesis centers on the appearance of tapetally derived orbicules that have the identical spinule ornament as mature pollen grains (Pl. 3, Fig. 2). Thus, in the case of these *Classopollis* grains, the majority of pollen wall development was controlled by the grain protoplast, whereas the final ornament is the result of tapetal activity controlled by the sporophyte.

Rowley & Srivastava (1986) have demonstrated that the sporoderm substructure in at least one species of *Classopollis* consists of radially oriented rods formed by five subunits that are in turn enveloped by a binder. Although this study utilized dispersed *Classopollis* grains and thus does not trace the stages of sporoderm ontogeny, it is highly significant in demonstrating pollen wall preservation at the substructural level. In the limited number of taxa that have been studied at this level of resolution, it appears that there is some uniformity in the structure of sporopollenin receptors, but that they differ depending on their location in the sporoderm (Rowley 1991). Moreover, it is increasingly apparent that the manner in which pollen grains develop and enlarge is highly variable within major groups of plants, and thus may be of limited value in establishing phylogenetic homologies.

Another example that demonstrates the in situ preservation of sporoderm substructure involves the megaspores of several *Selaginella* species. W. A. Taylor (1989) demonstrated

PLATE 1

1 Longitudinal section of *Cyathotheca tectata* sporangium containing a large number of spores; 58x.

2 Section of two *Gothania lesliana* pollen sacs with clumps (arrows) of immature pollen grains. T=tapetal membrane and epidermis surrounding pollen grains; 200x.

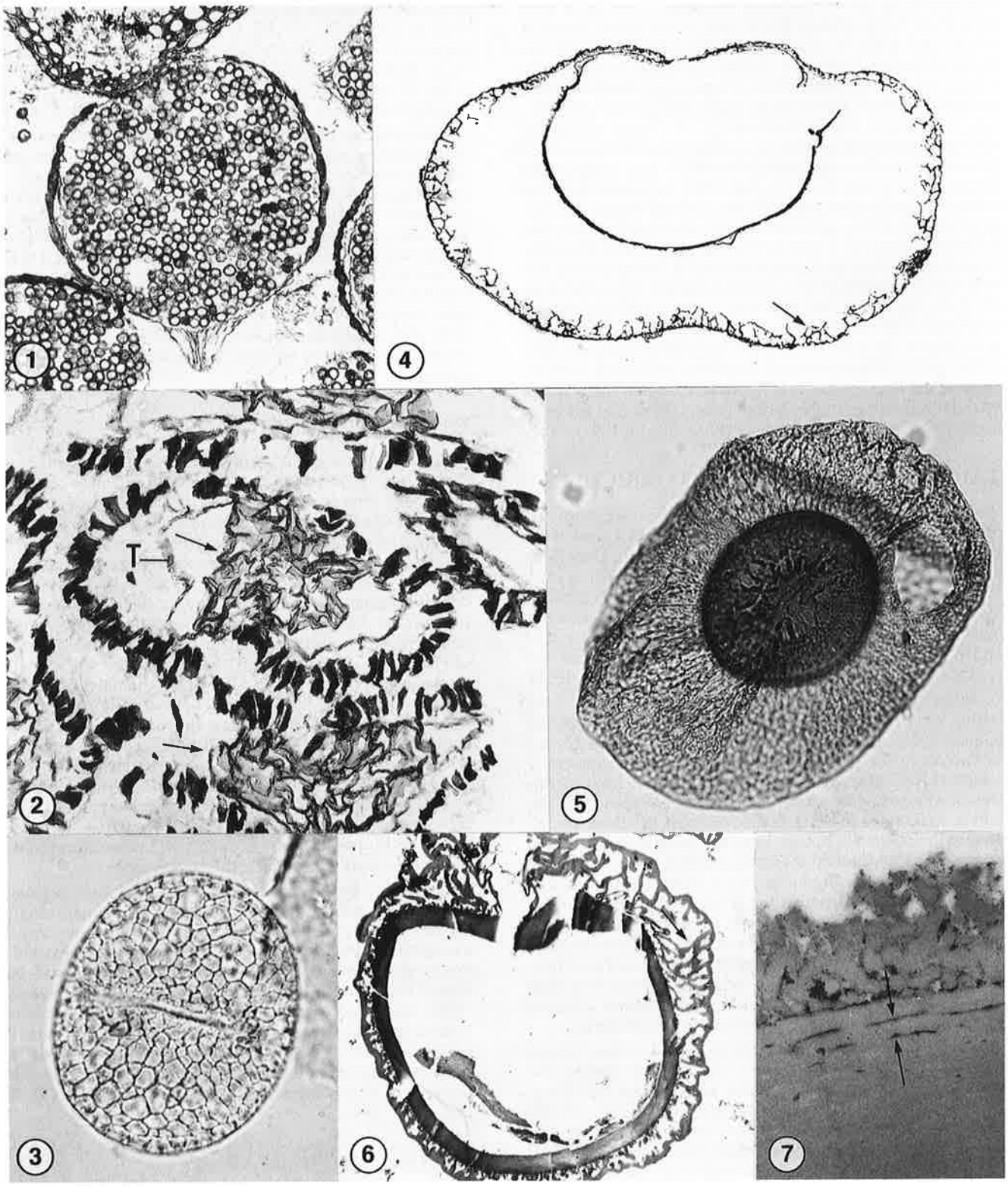
3 Distal surface of *Vesicaspora* pollen grain showing endoreticulations within sacci; 1000x.

4 Ultrathin section of mature *Felixipollenites* grain showing saccus/corpus attachment on proximal surface. Arrow indicates endoreticulations; 700x.

5 Proximal surface of *Felixipollenites* grain. Note saccus endoreticulations; compare with those in Figure 4; 500x.

6 Ultrathin section of *Sertostrobus laxus* pollen grain showing continuous sporopolleninous threads of protosaccus (arrow); 7000x.

7 Section of *Potoniea carpentieri* sporoderm showing nexine lamellae (between arrows); 30 000x.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that among the extant species of the genus there are at least three basic types of megaspore wall construction, some of which also occur in fossil dispersed megaspores (W. A. Taylor & Taylor 1988). In *S. galeottii*, a major portion of the megaspore wall is constructed of repeating plate-like units, each 600 nm thick, that form an organized patchwork structure throughout the sporoderm (W. A. Taylor & Taylor 1987a). Because this pattern of megaspore wall construction is found in modern species of *Selaginella* that produce the largest megaspores, W. A. Taylor (1989) suggested that this subunit organization provides the optimal means for megaspore expansion, perhaps due to shearing between the individual modular components. The presence of an identical pattern in some fossil megaspores (e.g. *Horstisporites*) has been useful in relating these dispersed spores to modern taxa (Pl. 3, Fig. 4), and in documenting the presence of a unique developmental pattern of megasporogenesis at a particular point in geologic time. Because this sporoderm pattern occurs in the largest megaspores of *Selaginella*, including some as early as the Cretaceous, it is hypothesized that there was a selective advantage in this ontogenetic pattern that has been maintained in some modern taxa (W. A. Taylor 1991).

TAPETAL MEMBRANES AND ORBICULES

In modern plants, orbicules (Ubisch bodies) are produced on the radial and tangential walls of tapetal cells, as one of the byproducts of a secretory tapetum (Pacini 1990). They have been variously classified as to size and shape (Chen *et al.* 1988), and in general have the same ornament as is present on mature pollen grains. Although the function of orbicules has been variously interpreted, it is now clear that in some extant and fossil taxa orbicular sporopollenin is added to the mature pollen exine during ontogeny (Taylor 1982; Kurmann 1991).

In the fossil record, orbicule-like deposits are found adhering to spores of some of the oldest spore producing plants (Gensel 1980), and this still happens in many major groups extending to the present. Although it had been generally assumed that orbicules were produced only in seed plants, similar appearing structures have also been reported in extant ferns (Lugardon 1981). Some orbicules, like those associated with *Classopollis* pollen, have the same type of external ornament as is found on the mature pollen grains (Pl. 3, Fig. 2). In this example (Taylor & Alvin 1984), the presence of ornamented and unornamented orbicules provides a convenient method to monitor changes in pollen wall development, as well as to trace the origin of sporopollenin. Because orbicules represent the developmental activities of a particular type of tapetal system (i.e. secretory), recording their existence provides important, indirect data about different patterns of microsporogenesis through geologic time.

In addition to orbicules, in situ spore and pollen macerations also yield a variety of membrane systems (peritapetal membranes), which are associated with the tapetum (Pl. 3, Fig. 5). Although few have been extensively investigated, it is clear that they are highly variable and may provide still another parameter that can be used to characterize the ontogeny of fossil pollen and spores through time. For example, in sporangia of the seed fern pollen *Schopfipollenites*, the tapetal membrane system is arranged in stacks (Pl. 3, Fig. 3), with each membrane system constructed of three distinct units (Taylor 1976a, b). The innermost unit has two parts, each uniformly 0.02 μm thick, and separated by randomly positioned beads of electron dense material. An irregularly thick component is present on the outside of this layer. This type of organization differs from that described for sporangia producing *Classopollis* (Taylor & Alvin 1984). In the latter the organization is distinctly bifacial with a smooth, electron dense outer layer and thicker, less dense inner component (Pl. 3, Fig. 6). At some levels, distinct globular elements unite the tapetal membranes with developing orbicules (Pl. 3, Fig. 7).

Few studies have been done on tapetal membranes in extant plants, and thus little is known about their function. Heslop-Harrison (1969) suggested that the membrane is an enclosing sac for the developing microspores, whereas Dickinson (1971) and Keijzer (1987) hypothesized that the membrane may be some form of dispersal system within the pollen sac. There are few reported examples of tapetal membranes in fossils, and only for *Classopollis* pollen has it been possible to suggest that these membranes are associated with orbicule production (Pl. 3, Fig. 7; Taylor & Alvin 1984). As with studies of orbicules, the investigation of fossil tapetal membranes can only be carried out with in situ pollen and spores.

ENIGMATIC FOSSILS

The biological affinities of some fossil plants remain unknown despite the presence of abundant, and often complete, specimens. One example is *Protosalvinia*, a compressed, Upper Devonian thallus-like structure that historically has been assigned to several taxonomic groups, ranging from the Phaeophyta to a hypothetical alga exhibiting terrestrial adaptations (Niklas & Phillips 1976). In some specimens oval depressions contain tetrads of spores, each of which may range up to 250 μm in diameter. The spores are difficult to detach from one another and from the thallus. The spore wall of *Protosalvinia* is constructed of an outer zone with lamellae in the contact region (Pl. 4, Fig. 1), and an inner, more homogeneous zone (W. A. Taylor & Taylor 1987b). A distinct trilete mark and sutures indicate the meiotic origin of these spores. When their sporoderm organization is compared with that of tetraspores found in certain extant brown algae, the group with which many believe *Protosalvinia* has the closest affinities based on thallus morphology, there are no ultrastructural similarities. A detailed analysis of in situ spores of this fossil does not identify its taxonomic affinities, but does appear to eliminate the brown algae.

Parka decipiens is another enigmatic Devonian organism for which the botanical affinities remain problematic, in part because it is impossible to determine whether the spores are meiotic products. The wall of in situ spores is constructed of two layers: an outer homogeneous zone and inner lamellate layer (Hemsley 1989). Based on these observations, Hemsley (1990) suggested that the spores of *Parka* are intermediate between the oospores produced by some algal group and the haploid, triradiate spores of certain bryophytes. Thus, the close examination of in situ *Parka* spores suggested an alternative hypothesis regarding the botanical affinities of this organism.

TAXONOMIC VARIABILITY

One of the most difficult problems in attempting to gauge the nature of past vegetation on the basis of dispersed pollen grains and spores is the inability to distinguish between developmental differences and those that reflect species. This has resulted in an extensive list of genera and species, some of which clearly represent variability within a single biological taxon. For some *sporae dispersae* taxa this is a difficult

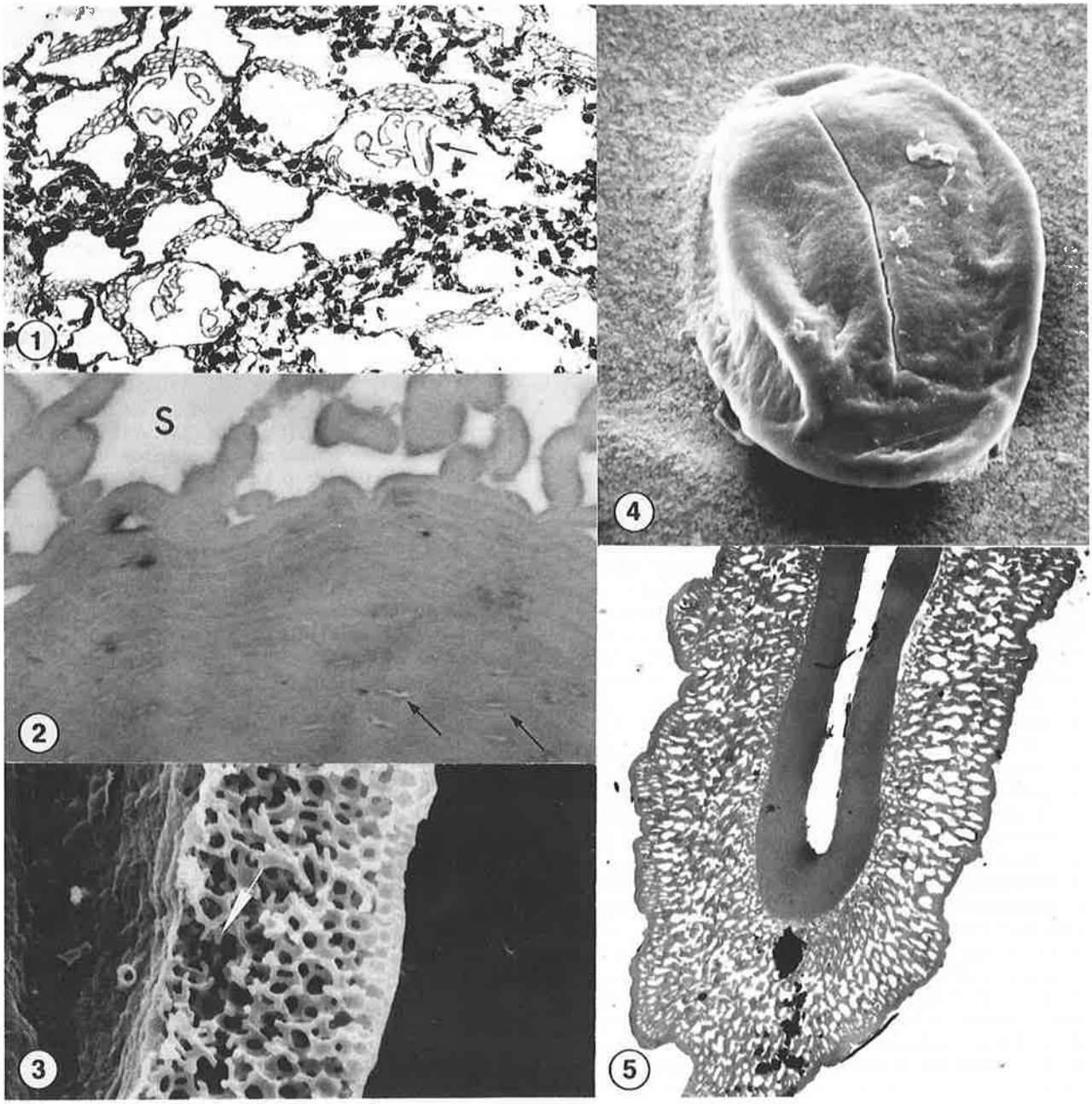


PLATE 2

1 Several *Bernaultia* pollen sacs in transverse section containing *Schopfipollenites* grains (arrows). The presence of sclerenchyma between some of the pollen sacs provides an independent measure of pollen organ development; 28x.

2 Part of sporoderm of *Schopfipollenites* in transverse section showing nexine lamellae and lumina of sexine (S). Arrows indicate regions where lamellae are only slightly separated; 82 000x.

3 Fractured sporoderm of *Schopfipollenites* showing alveolate sexine in which elements have separated (arrow) near nexine (left); 4000x.

4 Proximal surface of *Schopfipollenites* grain showing median deflection of monolete suture; 200x.

5 Sporoderm of *Schopfipollenites* grain showing inner homogeneous nexine and outer alveolate sexine. Compare with Figure 3; 3000x.

problem to resolve, especially where a continuum of minor morphological differences may extend over a wide geographic range and/or through a considerable segment of geologic time. The ability to assess variability within pollen and spore taxa, and thereby to establish taxonomic limits, is one of the major contributions of in situ studies.

It is often possible to obtain information on a variety of parameters, ranging from grain size to minute details regarding ornamentation, from a population of grains analyzed from a single sporangium. Sporangia can be sampled from most individual reproductive organs so that a range can be established for each morphological character. In situ grains provide the opportunity to identify, for example, developmental stages that might otherwise obscure the variability of mature grains.

The correct morphological interpretation of a mature pollen grain or spore is another area where in situ studies provide important information that is unavailable from other sources. The spores produced by Carboniferous sphenophytes offer a good example of this approach. For example, *Calamospora* is the genus most often associated with arborescent calamites, but this type is also reported to have been produced by other groups (Traverse 1988, p. 182). These trilete spores include forms with a wide range of sizes, even including megaspores (Pl. 4, Fig. 2). One important generic character is the smooth spore wall. In studies of in situ calamitean spores such as those of *Calamostachys binneyana* (Pl. 4, Fig. 2), it is often difficult to obtain good specimens of *Calamospora* that are not obscured by what has been interpreted as sporangial or tapetal debris. In other calamitean cones, such as *Pendulostachys cingulariformis* (Pl. 4, Fig. 6), the spores are so tightly packed within the sporangium that it is difficult to identify the outer limit of the wall. Spores within most calamitean cones are associated with extraexinous appendages or elaters (Pl. 4, Fig. 6; Good & Taylor 1974, 1975). It is these elaters that constitute the sporangial "debris" seen in almost all calamitean cones. *Calamospora* spores with elaters attached are circumscribed by the rare *sporae dispersae* taxon *Elaterites triferens* (Wilson 1943). Good (1975) indicated that some calamitean sporangia (e.g. *Calamocarpon insigne*) contain spores with elaters tightly coiled around the spore body (Pl. 4, Fig. 3), as well as spores without elaters. He suggested several possible explanations for this seemingly unusual condition, including the mechanical separation of the elaters prior to or during dispersal (Pl. 4, Fig. 8), or elater removal during preparation. These explanations may account for differences in the morphology of some mature calamitean spores, but the main reason for the presence and absence of elaters on spores within a single sporangium is developmental. Good (1975) showed that *Vestispora* may be interpreted as a *Calamospora* spore in which the elaters are tightly coiled around the body. If the elaters are fully expanded, the spore fits the generic diagnosis of *Elaterites*; if they are missing the spore is of the *Calamospora* type. Irrespective of the biological implications of elaters and how they may have functioned in the calamites, in situ studies have shown that most Carboniferous calamites produced elater bearing spores much like those of modern *Equisetum*.

The presence or absence of another extraexinous layer, the perispore, also determines to which genus of dispersed spores certain sphenophyllalean spores should be assigned (Pl. 4, Fig. 7). For example, if the perispore is preserved, the spores of *Sphenostrobus iowensis* are referred to as *Vestispora*; if it is lacking, spores are *Calamospora* (Good 1978). If the perispore of *Peltastrobus* is present the spores may be included in *Columnisporites*; if this layer is lost or absent, the spores are classified as *Laevigatosporites*.

In situ spores of the Sphenophyllales are structurally and morphologically varied (Pl. 4, Fig. 7; W. A. Taylor 1986). All taxa but one have some form of perispore, which is highly variable within the group. Ultrastructurally, however, there is little similarity between sphenophyllalean spores and those of the calamites except that in both an extraexinous layer (perispore or elaters) may be present. The functional significance of this sporoderm component within the Sphenophyta is not fully understood; however, these structures probably represent adaptations for differing habitats or reproductive strategies (W. A. Taylor 1986). Our limited knowledge of the relationships among spores in this group has resulted from studies of in situ spores.

Because there are numerous fossil sphenophytes and one extant genus (*Equisetum*), developmental spore features can be directly compared. One variation is the number of elaters on the spore – three in the known fossil representatives (Pl. 4, Fig. 8), and two pairs (four) in *Equisetum*. Another distinction is the difference in sporoderm thickness between *Elaterites* (Kurmann & Taylor 1984a) and *Equisetum* (Lugardon 1969). The thickened perispore in the fossil may have served primarily to protect the exospore, and later may have become adapted as an aid to dispersal by helping spores to clump together through entanglement of the elaters, thereby increasing the effective surface area of the clump. This would ensure as well that several gametophytes would develop in close proximity.

PHYLOGENETIC IMPORTANCE

There are many examples in the literature in which features of pollen grains and spores have been used to infer phylogeny. Most such evolutionary proposals have been

PLATE 3

1 Ultrathin section through unspecialized portion of *Classopollis* sporoderm showing lamellate nexine (N), and columellate sexine (S) with supratectal spinules; 20 000x.

2 Section of *Classopollis* sporoderm with associated orbicules (arrows). Note identical ornamentation of orbicules and pollen wall; 7000x.

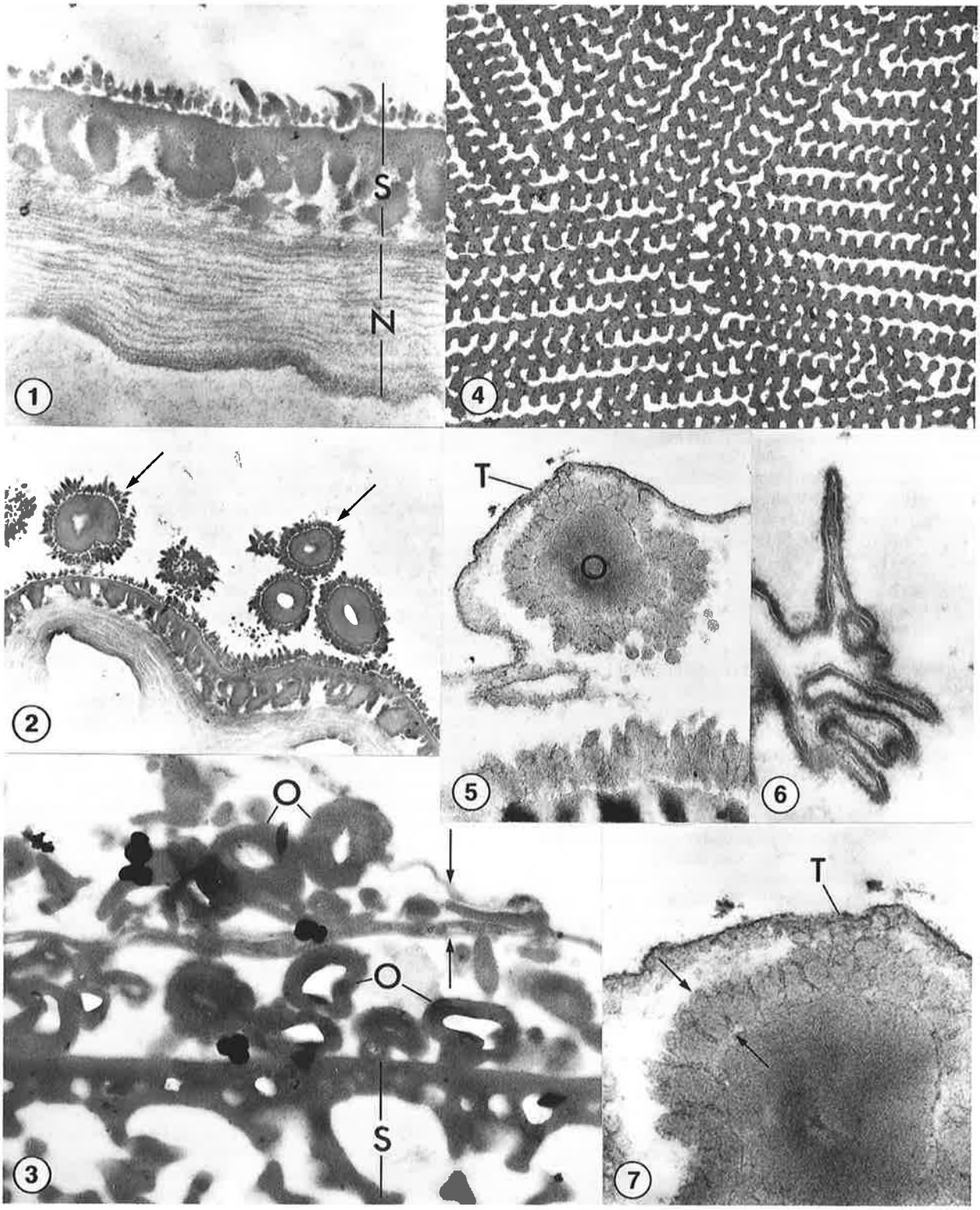
3 Several stacks of hollow orbicules (O) on surface of *Schopfipollenites* (S) grain. Some orbicules are stacked between membrane systems. Note complex nature of tapetal membrane (between arrows); 25 000x.

4 Ultrathin section through sporoderm of *Horstisporites* (Cretaceous) showing repetitive patchwork units of wall; 7000x.

5 *Classopollis* tapetal membrane (T) associated with a developing orbicule. Note immature pollen grain wall at bottom of figure. Compare with Figure 1; 20 000x.

6 Detail of *Classopollis* tapetal membrane showing bifacial configuration; 40 000x.

7 Enlarged orbicule from Figure 5 showing relationship between tapetal membrane (T) and globules of sporopollenin (between arrows); 50 000x.


S
N
1
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T
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based on dispersed grains, and have involved such characters as size, shape, number and nature of the apertures, sporoderm ultrastructure, and character of the ornament (Doyle 1988). For example, the direct angiosperm ancestor has historically been assumed to have possessed monosulcate pollen because this type of pollen was produced in a number of gymnosperm groups (Doyle 1978). Similarly, Walker & Walker (1984) hypothesized that the tectate columellate sporoderm found in most angiosperms has been derived from a granular sporoderm of the type present in some extant angiosperms suggested as being the most primitive. Others suggested a more complicated scenario in which the granular exine infrastructure represents a secondary reversal in some groups (Ward *et al.* 1989). As additional information has been assembled about the ultrastructure of extant and fossil pollen, it has become apparent that features of the pollen grain alone can not be used effectively to reconstruct evolutionary schemes for the whole plant. An excellent example is *Cyclusphaera psilata*, a Cretaceous diporate pollen grain. Ultrastructural studies of the sporoderm indicate radially aligned rods of sporopollenin that are morphologically identical to columellae of angiosperms, while other characters are more like those of certain gymnosperms (Taylor, Zavada & Archangelsky 1987). We believe that information regarding pollen development and the reproductive biology of the plant that produced *Cyclusphaera* pollen will also be required before the taxonomic placement of this grain type can be accurately determined.

In an attempt to identify which pre-Cretaceous monosulcate gymnosperm pollen grains might be related to the angiosperms, several authors (e.g. van Campo 1971; Doyle *et al.* 1975) have suggested that the gymnosperm nexine is homologous with the foot layer and endexine of angiosperms, and that the presence of nexine lamellae in gymnosperm pollen can be used to separate these two major groups of plants. Probably, however, these layers are not homologous (Zavada 1984). Moreover, the presence or absence of lamellae in any pollen grain may also be related to the ontogenetic level of the sporoderm, or even to the vagaries of electron microscope preparation. If fine structural details of pollen exines are studied over a wide range of developmental stages, ontogenetic differences may become distinguishable from those that may have phylogenetic significance. By such analyses, for example, the validity of the suggested homology between the endexine of angiosperms and nexine of gymnosperms (Guédès 1982) may be tested. However, to more fully understand the homology of mature sporoderm components, it is necessary to trace their developmental and evolutionary origins, by studying in situ fossils that represent a range of ontogenetic stages.

TERMINOLOGY AND TECHNIQUE

The study of pollen grains and spores relies on an often complex descriptive terminology. With the increasing utilization of transmission electron microscopy, new terms are being applied to describe the complexities of the sporoderm (Pl. 4, Fig. 4). Terms such as granular (Pl. 4, Fig. 5), alveolate, spongy, etc. are used differently by different researchers working on different scales. Where descriptive terms are combined (e.g. granulo-columellate) the problems of comparison become even more difficult. Standardization of descriptive terms seems necessary, and will be facilitated by descriptions that include a range of sporoderm structures and suites of developmental features.

A corollary to the importance of consistent terminology is the necessity of describing exine features based on ultrathin sections that are prepared in a predictable and repeatable manner (Pl. 4, Fig. 4). This is not always possible, especially where grains are small and difficult to manipulate, or where there are few specimens. Unfortunately, the sporoderm of far too many fossil pollen grains and spores has been characterized on only a few sections. Serial sectioning can insure that representative sections are obtained, and that a range of characters is available for analysis and comparison that include a variety of planes of section.

Another potential problem in interpreting the ultrastructure of pollen and spore exines is the introduction of stain artifacts. No standard methods are routinely used in the preparation of fossil pollen and spores, and this has the potential to cause major problems when attempting to determine homologous elements in sporoderm layers. For example, some research papers provide no information about preparation procedures, yet hypotheses are based on the presence or absence of certain wall layers. The problem is not a simple one that can be addressed by the adoption of standardized protocols, because unlike the spores and pollen of living plants, fossil grains have been subjected to varying degrees of diagenesis that may range from simple compaction to severe thermal alteration. With a sufficient number of sections it is possible to experiment with varying stain concentrations for different lengths of time to obtain consistent, optimum results. When attempting to identify delicate, ephemeral structures such as nexine lamellae, it is important

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PLATE 4

1 Ultrathin section of a *Protosalvinia* spore showing lamellae; 15 000x.

2 *Calamospora* spore macerated from *Calamostachys binneyana* cone; note smooth surface sculpture; 500x.

3 Microspore macerated from *Calamocarpon insignis* cone showing elaters tightly wrapped around spore body; 610x.

4 Sporoderm of *Cyclusphaera psilata* (Cretaceous) showing sexine rods in various planes of section; 18 000x.

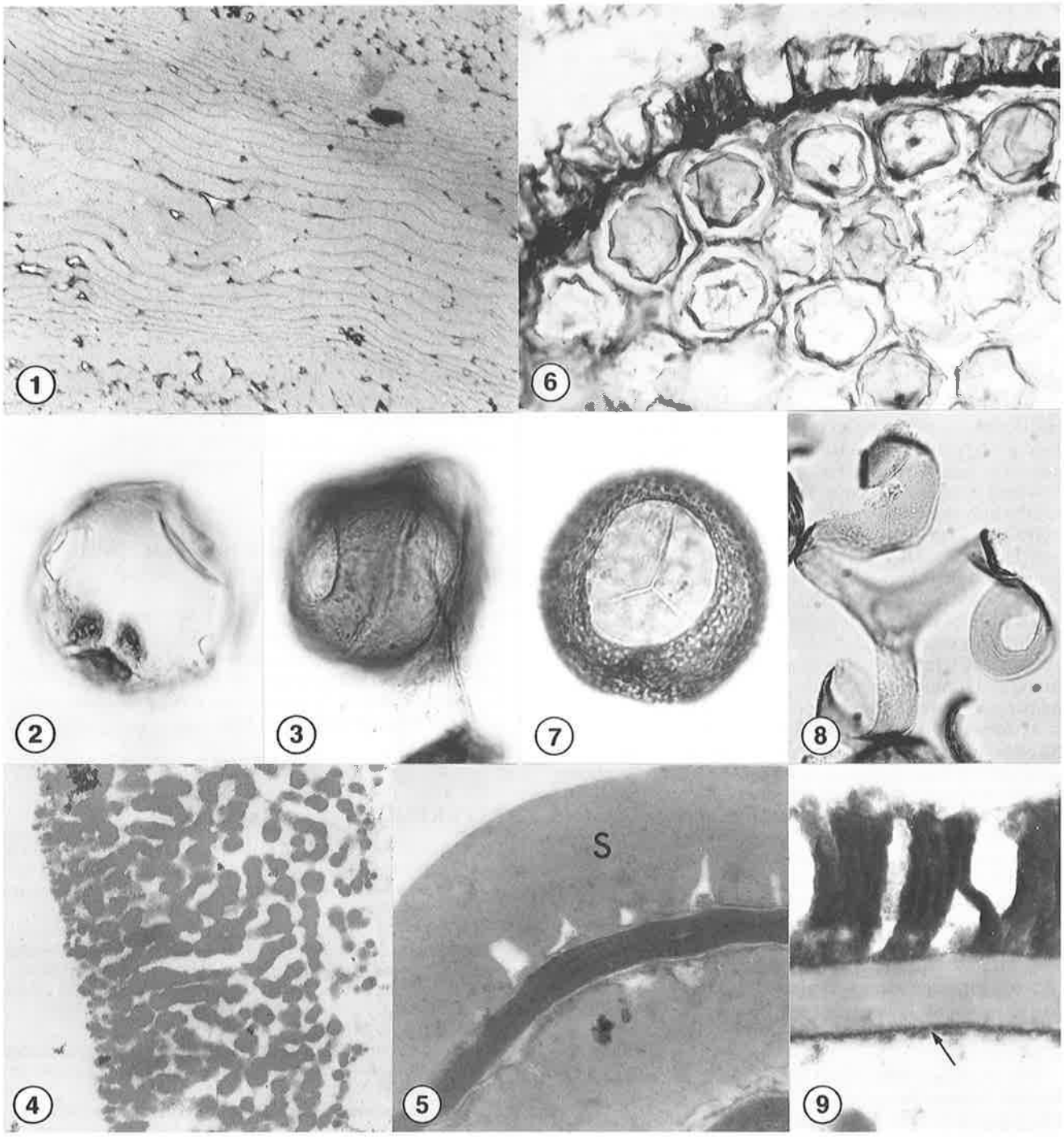
5 Compressed pollen grain of *Sahnia* showing homogeneous outer sexine (S) and granulate inner zone. The darkly stained zone is the nexine; 40 000x.

6 Sporangium of *Pendulostachys cingulariformis* with tightly packed spores, each enveloped by an outer sporoderm component (elater); 300x.

7 Proximal surface of *Sphenostrobus iowensis* spore with operculum removed to show trilete mark; 600x.

8 Isolated elater unit from a *Palaeostachya decacnema* spore; 370x.

9 Sporoderm of *Sentistrobus goodii* showing bilayered organization. Arrow indicates excessive stain deposition along inner surface; 30 000x.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to obtain information by using many combinations of stain schedules and section thicknesses, as Taylor & Rothwell (1982) did in their description of nexine lamellae in *Schopfipollenites*. Although this grain type has been sectioned by many workers, nexine lamellae have only been identified once in a very small number of specimens.

Excessive staining for transmission electron microscopy may cause residual artifacts that may be mistaken for wall layers. For example, in sphenophyte spores of *Sentistrobus goodii*, some residue is present along the inner region of the sporoderm close to the lumen (Pl. 4, Fig. 9), suggesting that there is a subdivision within the nexine. Examination of many grains and reduction of excess stain would tend to facilitate identification of these residues as artifacts, rather than sporoderm components.

CONCLUSIONS

Structural characters of fossil pollen and spores are the results of a long and complex series of genetic, biological and often geological interactions that must be considered in the analysis of these features. Studies based on numerous grains recovered from reproductive organs of known affinity provide the only method by which dependable information can be obtained about certain biological and evolutionary parameters. The fact that two pollen grains may have similar characters does not always indicate that they are taxonomically related, or that such characters had similar functions. Neither does the absence of certain features necessarily signify conceivably important differences. The study of fossil pollen and spores must, where possible, examine all characters representing early ontogeny and subsequent developmental states, and consider their functional roles and evolutionary significance. As new imaging systems offer increased resolution, it will be necessary to standardize techniques and terminology so that precise homologies can be established that reflect both development and evolution. As in situ pollen and spores are better understood, they can be more accurately compared with the more commonly encountered dispersed palynomorphs. Thus, for example, it will be possible to more accurately define past floras based on palynomorph signatures, and to better evaluate biogeographical and paleoecological provenances. All of these dimensions will contribute to a better understanding of the biology and the geological distribution of past floras, and to the evolutionary relationships among major groups of plants.

ACKNOWLEDGMENTS

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List of taxa

Bernaultia Rothwell & Eggert 1986
Bernaultia sclerotica (Baxter) Rothwell & Eggert 1986
Calamocarpon insigne Baxter 1963
Calamospora Schopf, Wilson & Bentall 1944
Calamostachys binneyana (Carruthers) Schimper 1869
Callistophyton Delevoryas & Morgan 1954
Caytonanthus Harris 1937
Classopollis Pflug 1953
Classostrobus comptonensis Alvin, Spicer & Watson 1978
Columnisporites Peppers 1964
Cordaianthus concinnus Delevoryas 1953
Cyathotheca tectata Taylor 1972
Cyclusphaera Elsik 1966
Cyclusphaera psilata Volkheimer & Sepúlveda 1976
Elaterites Wilson 1943
Elaterites triferens Wilson 1943
Equisetum Linnaeus
Felixipollenites Millay & Taylor 1974
Florinites Schopf, Wilson & Bentall 1944
Gothania Hirmer 1933, emend. Daghlian & Taylor 1979
Gothania lesliana Daghlian & Taylor 1979
Horstisporites Potonié 1956
Laevigatosporites Ibrahim 1933
Monoletes Ibrahim ex Schopf 1936
Palaeostachya decacnema Delevoryas 1955
Parasporites Schopf 1938
Parka Fleming 1831
Parka decipiens Fleming 1831
Peltastrobus Baxter 1950
Pendulostachys cingulariformis Good 1975
Phacelotheca Meyer-Berthaud & Galtier 1986
Potoniea carpentieri Zeiller 1899
Protosalvinia Dawson 1884
Sahnia Vishnu-Mittre 1953
Schopfiangium Stidd, Rischbieter & Phillips 1985
Schopfipollenites Potonié & Kremp 1954
Selaginella Beauvois
Selaginella galeottii Spring
Sentistrobus goodii Riggs & Rothwell 1985
Sertostrobus laxus Grauvogel-Stamm 1969
Sphenostrobus iowensis Levittan & Barghoorn 1948
Vesicaspora Schemel 1951, emend. Wilson & Venkatachala 1963
Vestispora Wilson & Hoffmeister 1956

N.B. Taxa tabulated in Table 1 are not included in "List of taxa".

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