

THE ULTRASTRUCTURE OF SAHNIA POLLEN (PENTOXYLALES)¹

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The micromorphology and fine structure of in situ pentoxylalean pollen are described from the holotype of *Sahnia laxiphora* Drinnan and Chambers 1985 collected from the Lower Cretaceous (Valanginian-Aptian) of Victoria, southeastern Australia. Pollen grains are ovoid, monosulcate, and relatively small, averaging 26 μm in length. Exine ornamentation is psilate. The sporoderm is two-parted with the sexine staining lightly throughout and approximately six times the thickness of the more darkly staining nexine. The exine over the sulcus is typically strongly invaginated, and may or may not include an extremely thin sexine layer. The outer part of the sexine is homogeneous, while the inner part is composed of relatively large granules separated by irregular lacunae of various sizes; lacunae are most pronounced at the sexine-nexine interface. Faint lamellae characterize the nexine in both apertural and nonapertural regions. Granular orbicules are often associated with the exine surfaces and also occur appressed to pollen sac walls along with lamellated tapetal membranes. Sporoderm ultrastructure is compared to that of nonsaccate pollen of other groups, and particularly to pollen of Bennettitales, Gnetales, angiosperms, and similar plants, to which the Pentoxylales have been thought to be closely related. Although *Sahnia laxiphora* pollen is not identical to that of any of these taxa, the strongest similarity is with pollen of Bennettitales.

The Pentoxylales were established in 1948 for silicified gymnospermous plant remains from Jurassic rocks at Nipania in the Rajmahal Hills, Bihar Province, northeastern India (= Pentoxyleae; Sahni, 1948). Since that time, there have been several additional studies of the Rajmahal material (Vishnu-Mittre, 1953; Rao, 1974, 1976, 1981; Stewart, 1976; Bose, Pal, and Harris, 1984, 1985), and numerous compression fossils from Southern Hemisphere localities of Mesozoic age have also been assigned to the group (e.g., New Zealand, Harris, 1962, 1983; Australia, New South Wales, White, 1981 [see also Walkom, 1921]; Queensland, S. Turner, personal communication; Victoria, Drinnan and Chambers, 1985, 1986 [see also Douglas, 1969]). Four genera have been established: *Pentoxylon* for the characteristic woody stems, *Carnoconites* for ovulate organs, *Sahnia* for microsporangiate organs, and *Nipaniophyllum* for leaves. Although not all of these plant parts have been found connected, the suite of organs is often collectively referred

to as the *Pentoxylon* plant (for review see Bose, Pal, and Harris, 1985; Crane, 1985, 1988).

The pollen-producing organs of the Pentoxylales were initially described by Vishnu-Mittre (1953) from the Rajmahal Hills. *Sahnia nipaniensis* consists of numerous filiform microsporophylls, each 1–2 cm in length, borne on a *Pentoxylon*-type spur shoot. The microsporophylls (= microsporangiphores sensu Bose, Pal, and Harris, 1985) were originally thought to be whorled and fused at their bases to form a cup (Vishnu-Mittre, 1953). However, Rao (1974, 1981) and Bose, Pal, and Harris (1985) have shown that the microsporophylls are not fused proximally, but rather borne either irregularly or in a spiral on a collarlike structure surrounding the conical shoot apex (see also Drinnan and Chambers, 1985). Each microsporophyll consists of a single main branch bearing numerous short branches on all sides. The side branches bear four to seven unilocular, pyriform sporangia borne on short stalks. The sporangium wall is a single cell thick with a possible line of dehiscence marked by cells with thickened periclinal walls (Vishnu-Mittre, 1953). A second species of *Sahnia* (*S. laxiphora*) based on compression material from the Lower Cretaceous of Australia is similar in morphology to *S. nipaniensis* (Drinnan and Chambers, 1985, 1986).

Pollen grains from *Sahnia nipaniensis* microsporangia were initially described as boat-shaped, monocolpate with a smooth wall, and

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averaging $25\text{--}26 \times 10\text{--}25 \mu\text{m}$ in size by Vishnu-Mittre (1953). However, the preservation of pollen grains in the *Sahnia* material from the Rajmahal Hills is generally poor (Bose, Pal, and Harris, 1985), and examination of pentoxylalean pollen beyond these original observations is especially sparse. Sukh-Dev (1980) isolated in situ pollen from the type material of *S. nipaniensis* and compared these grains with other dispersed pollen from Rajmahal Hills rocks using transmitted light microscopy. The pollen from *S. nipaniensis* was found to most closely resemble the sporae dispersae genus *Cycadopites* (see Sah and Jain, 1964); pollen isolated from Australian material of *S. laxiphora* has also been compared with this dispersed pollen genus (M. E. Dettmann [personal communication] in Douglas, 1969, p. 242).

Preliminary fine structural analyses of *Sahnia* pollen, employing electron microscopy, were provided by Taylor and Taylor (1987) and Taylor (1988) as part of a comprehensive review of sporoderm ultrastructure in fossil gymnosperms. The present study expands these earlier observations, provides additional details of the ultrastructure and micromorphology of in situ *Sahnia laxiphora* pollen grains, and contributes new data with which to assess the systematic affinities of the Pentoxylales.

MATERIALS AND METHODS

Several pollen organs assigned to *Sahnia laxiphora* Drinnan and Chambers are known from the Lower Cretaceous (Valanginian-Aptian) of southeastern Victoria, Australia (Drinnan and Chambers, 1985, 1986). Pollen grains described and illustrated in this paper were isolated from a single specimen collected from the Strzelecki Group exposed at the Whitelaw road cutting (see Douglas, 1969; Drinnan and Chambers, 1985 for locality details). This specimen was first described and illustrated as "fertile organ bearing microsporangia" (Douglas, 1969, pl. 45, Figs. 1, 2, pl. 46, Figs. 1, 6, pl. 48, Fig. 1, pl. 51, Fig. 1, text-Figs. 5.2–5.6), but it was subsequently redescribed, reillustrated, and taken as the holotype of a new species, *Sahnia laxiphora* Drinnan and Chambers (1985). Part and counterpart of the specimen were originally assigned Geological Survey of Victoria numbers (GSV 60003, 60004, light microscope preparations listed under other numbers by Douglas, 1969), and are now housed in the paleobotanical collections of the National Museum of Victoria (NMV P167524).

Both part and counterpart of the specimen show an obliquely compressed pollen organ

consisting of an aggregation of microsporophylls each bearing numerous sporangia in their distal portion. Entire compressed pollen sacs containing in situ grains were isolated from the specimen using standard maceration techniques. Pollen sacs and individual pollen grains were examined with light microscopy (LM) as well as scanning and transmission electron microscopy (SEM and TEM).

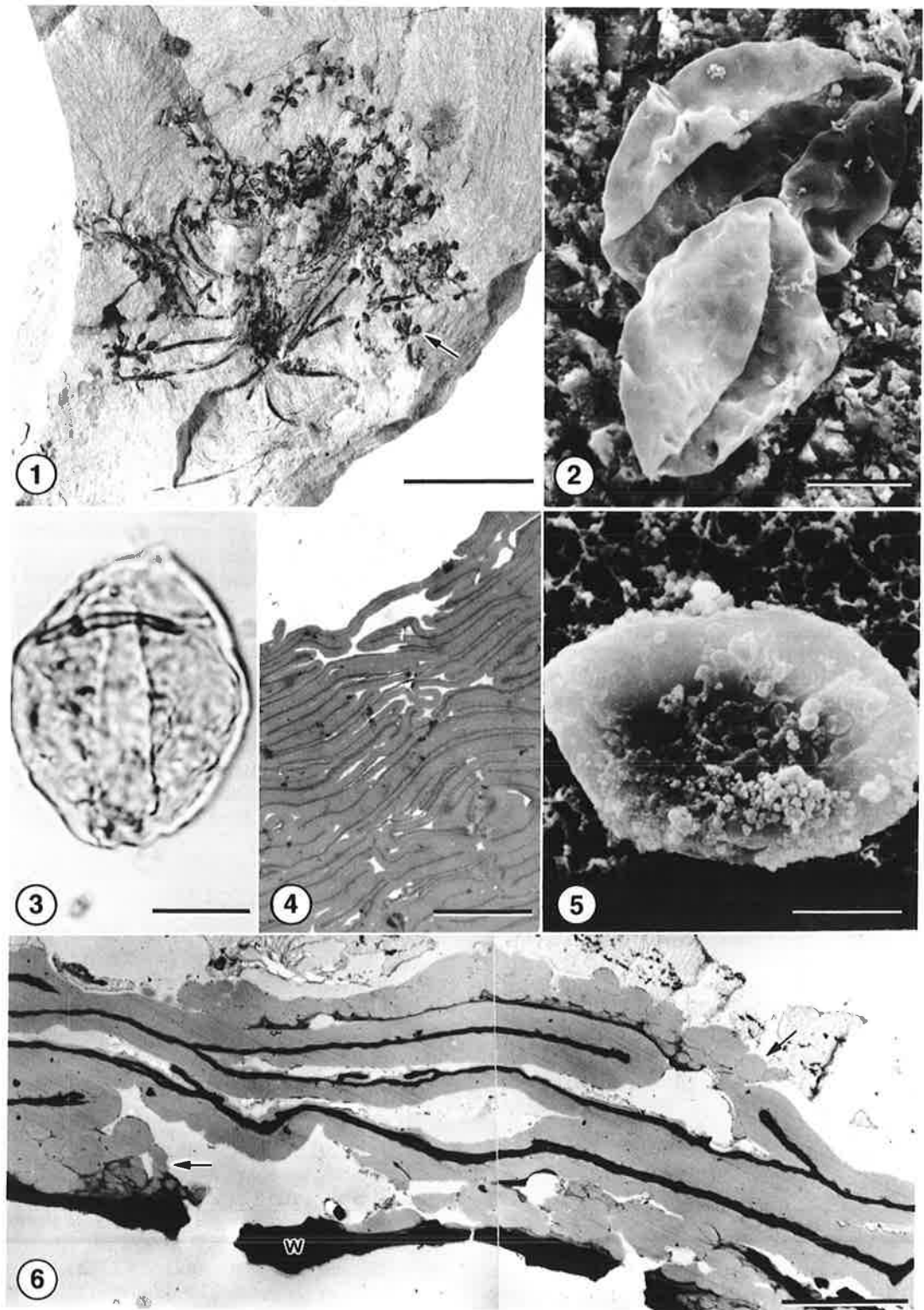
Pollen grains for LM were prepared according to standard palynological protocols (Doher, 1980), mounted on glass microscope slides, and examined on a Zeiss Ultraphot light microscope. Specimens for SEM were either pipetted directly onto aluminum stubs or through cellulose filters under suction, which were then mounted on stubs. Specimens were coated with gold-palladium and examined on a Hitachi S-500 scanning electron microscope at an accelerating voltage of 20 kV. Additional fossils, for TEM, were also pipetted onto cellulose filters under suction and subsequently coated on both sides with agar. The agar-embedded filters were dehydrated in a graded ethanol series, transferred to 100% acetone (with four changes to ensure complete filter removal), and gradually infiltrated with Spurr low viscosity epoxy resin and embedded. Ultrathin sections were cut with a diamond knife, collected on uncoated copper slot grids, and dried onto form var support films (Rowley and Moran, 1975). Grids were stained with 1% potassium permanganate, 1% uranyl acetate, and lead citrate (Venable and Coggeshall, 1965), and examined with a Zeiss EM-10 transmission electron microscope at 60–80 kV.

RESULTS

Sahnia laxiphora consists of a short length of axis bearing numerous (> 30) microsporophylls. Microsporophylls are unbranched for most of their length, but in their distal half they bear numerous simple, spherical to ovoid pollen sacs, each on a short stalk (Fig. 1). Occasionally, short side branches of the microsporophyll have more than one attached pollen sac. Pollen sacs contain numerous, highly compressed in situ pollen grains (Fig. 4). The walls of the pollen sacs can be recognized but are not well preserved (Figs. 6, 10).

Pollen grains are small, ovoid, and monolucate. In polar view the grains measure $24(26)28 \mu\text{m}$ in length and $20(23)25 \mu\text{m}$ in breadth (Figs. 2, 3, 5). The sulcus is relatively broad, and the exine in this region is often strongly invaginated. Exine ornamentation is psilate (Figs. 2, 3).

The pollen wall is composed of two distinct



Figs. 1-6. *Sahnia laxiphora* Drinnan and Chambers (NMV P167524). 1. Morphology of pollen organ showing several microsporophylls and simple pollen sacs (arrow). Bar = 1.0 cm. 2. Distal view of two pollen grains showing psilate exine surface; note the strongly invaginated exine over the sulcus of the lower grain. SEM. Bar = 7.5 μ m. 3.

layers, with an outer sexine approximately six times the thickness of an inner nexine (Figs. 6–9). The sexine has a variable affinity for heavy metal stains but generally stains lightly throughout. The sexine is relatively thin, averaging $0.82\ \mu\text{m}$ in thickness, and in many specimens consists of an inner granular layer grading into an outer ultrastructurally homogeneous layer. The inner layer consists of relatively large granules (approx. $0.12\ \mu\text{m}$ in diam) separated by irregular lacunae of variable sizes. Exine granules have approximately the same size, shape, and staining density as the granular elements composing orbicules associated with the surfaces of grains and pollen sac walls (see below). At the interface with the nexine, granules and lacunae are particularly pronounced (Fig. 8), often giving the appearance that the sexine is slightly separated from the underlying nexine (Figs. 7–9). The granules also vary considerably in their distinctness, in particular outer granules, where there is no clear separation from the more homogeneous outer part of the sexine. The consistency of wall construction in all grains examined suggests that the features described are not a result of preservational phenomena, but rather reflect differences in the nature of the sporopollenin wall.

The broad sulcus is clearly visible in ultrastructural sections. In some grains there is an extremely thin sexine layer overlying the nexine along the sulcus; this originates from a gradual, lateral thinning of the nonapertural sexine (Figs. 8, 9). In other grains, evidence of a sexine layer in this area is completely absent (Fig. 9).

The nexine stains more densely than the sexine (Figs. 6–9). This darkly staining layer averages $0.13\ \mu\text{m}$ in thickness, and is characterized by the occasional presence of faint lamellae, averaging $0.04\ \mu\text{m}$ thick. Lamellae may occur in both apertural and nonapertural nexine regions (Figs. 7, 8) and are typically most conspicuous close to the nexine/sexine interface. Apertures are often inconspicuous in section view because of the strongly invaginated sporoderm (Fig. 6). Folding of the apertural nexine is particularly complex, perhaps due to the absence of a sexine layer in this region of the grain. In some specimens the nexine appears to be inrolled independently of the sexine (Figs. 11, 12).

Tapetal membranes and orbicules frequently occur within pollen sacs. Lamellated tapetal membranes average $0.09\ \mu\text{m}$ in thickness, are typically appressed against the interior surface of the pollen sac walls, and are often associated with orbicules (Fig. 10). Although many orbicules have variable shapes in section view, most are circular to oval and range from 0.29 to $0.71\ \mu\text{m}$ in diameter. Ultrastructurally, orbicules are similar to the sexine, although they have a more distinct granular structure (Figs. 6, 9, 10). Orbicules are also found appressed against the exine surfaces of some grains (Fig. 5).

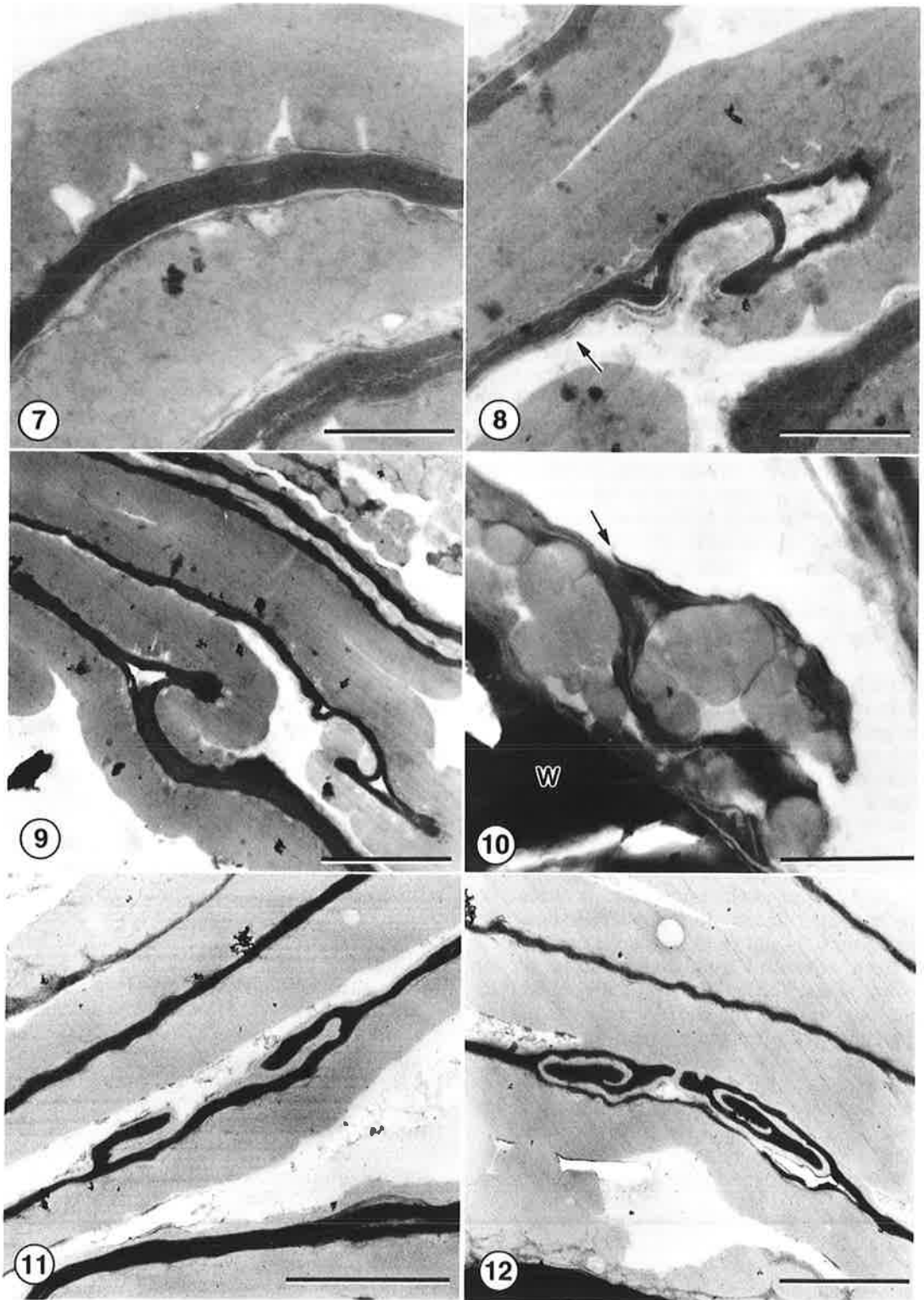
DISCUSSION

Comparison with extant and fossil taxa—Details now available on the structure of *Sahnia* pollen remove an important gap in previous knowledge of the Pentoxylales (Crane, 1985) and contribute to the accumulating information on the micromorphology and ultrastructure of in situ fossil gymnosperm pollen (Taylor and Taylor, 1987; Taylor, 1988). These new data therefore provide an improved basis for comparing the pollen of Pentoxylales with that of other seed plants.

Several features distinguish *Sahnia* pollen from the grains of other extant and fossil gymnosperms (Table 1). The absence of a saccus distinguishes *Sahnia* pollen from that of most conifers (including the earliest fossil representatives of the group), cordaites, and several groups of 'seed ferns' including Caytoniales, Corystospermales, and Glossopteridales (see Taylor and Taylor, 1987; Taylor, 1988 for review). *Sahnia* pollen is ovoid in shape and has a distal sulcus; this also distinguishes it from pollen of certain conifers that have spheroidal, inaperturate grains (e.g., *Araucaria*), as well as medullosan and lyginopterid 'seed ferns' in which the pollen has a proximal trilete or monolete mark rather than a distal sulcus (Taylor and Taylor, 1987; Taylor, 1988). Granular sexine organization distinguishes *Sahnia* pollen from that of cycads and *Ginkgo*, which are characterized by an alveolar sexine infrastructure (Audran and Masare, 1976, 1977, 1978; Audran, 1987; Dehgan and Dehgan, 1988; Hill, 1990). Excluding the Peltaspermales, for which details of pollen ultrastructure are not yet known

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Distal view of pollen grain showing broad sulcus. LM. Bar = $7.5\ \mu\text{m}$. 4. Numerous compressed in situ grains within one pollen sac; note thin nexine (dark staining) and thicker sexine (lighter staining). TEM. Bar = $5.0\ \mu\text{m}$. 5. Proximal surface of pollen grain with associated orbicules. SEM. Bar = $5.0\ \mu\text{m}$. 6. Transverse section through portion of a single pollen sac showing three in situ grains (one complete); note pollen sac walls (W), numerous orbicules associated with the walls of the pollen sac (arrows), and strongly invaginated exine at the sulcus. TEM. Bar = $2.5\ \mu\text{m}$.



Figs. 7–12. *Sahnia laxiphora* Drinnan and Chambers (NMV P167524). 7. High magnification of nonapertural sporoderm showing two-zoned sexine and compressed nexine; note homogeneous outer part of sexine, large granular units separated by irregular lacunae internally, and faint lamellae at the nexine surface. TEM. Bar = 0.5 μm . 8. High

(Taylor, 1988), these comparisons leave four groups of extant and fossil seed plants (Bennettiales, *Eucommiidites*-plants, Gnetales, and certain angiosperms) in which at least some taxa have ovoid pollen with a distal sulcus and a granular sexine infrastructure.

Eucommiidites pollen is easily distinguished from that of *Sahnia* by the presence of two prominent, lateral, groove-like thinnings in the exine, and the more rounded ends of these grains as seen in polar view. Pollen of extant Gnetales (except the inaperturate grains of *Gnetum*) is distinguished from that of *Sahnia* by the presence of prominent longitudinal plications. However, both *Eucommiidites* and gnetalean pollen, as well as pollen of Bennettiales and certain angiosperms, are similar to that of *Sahnia* in having a distinct granular component in the outer part of the sporoderm. Both within and among these groups the details of exine stratification vary considerably, particularly with regard to granule size and position with respect to the differentially stained sporoderm layers.

Eucommiidites pollen that occurs in the micropyles of seeds of *Erdtmanispermum balticum* (Pedersen, Crane, and Friis, 1989), as well as pollen from the fossil bennettitalean microsporophyll *Leguminanthus siliquosus* (Ward, Doyle, and Hotton, 1989), have the granular sporoderm layer separated from the darkly staining inner layer by a structurally homogeneous, lightly staining zone. Similarly, in certain angiosperms, for example the Early Cretaceous putative angiosperm grain *Lethomasites fossulatus* (Ward, Doyle, and Hotton, 1989), a very thin homogeneous layer (foot layer) may be present, although the darkly staining inner layer may be entirely absent. In contrast, in *Sahnia* pollen the granules are in direct contact with the darkly staining inner layer. A basically similar arrangement, but with finer granules, occurs in *Eucommiidites* pollen (Doyle, Van Campo, and Lugardon, 1975; Trevisan, 1980), including that isolated from *Erdtmanitheca texensis* (Pedersen, Crane, and Friis, 1989), pollen of the bennettitalean *Cycadeoidea dacotensis* (J. M. Osborn, unpub-

lished data) as well as pollen of extant *Welwitschia* and *Ephedra* (Gullvåg, 1966; Van Campo and Lugardon, 1973; Kedves, 1987). Pollen of *Cycadeoidea dacotensis* also lacks lamellae in the darkly staining inner sporoderm layer.

These comparisons show that pollen of *Sahnia laxiphora* is not unequivocally identical to any previously described in situ pollen, but it is clear that several characters of *Sahnia* pollen occur within a relatively small assemblage of seed plants including Bennettiales, Gnetales, *Eucommiidites*-plants, and certain angiosperms. Because *Sahnia* pollen lacks the specialized features that distinguish *Eucommiidites* and gnetalean grains (i.e., lateral grooves, longitudinal plications), it may be suggested that the strongest similarities are with the pollen of certain Bennettiales.

Systematic implications—Since the Pentoxylales were first described it has been recognized that they exhibit a unique combination of characters seen in several groups of seed plants (e.g., Sahni, 1948). Based on a number of vegetative and reproductive features, including the nature of pollen as seen through transmitted light, the Pentoxylales have been compared with a variety of gymnosperm taxa including Coniferales (Araucariaceae), Ginkgoales, Medullosales, and Bennettiales (e.g., Rao, 1981; Bose, Pal, and Harris, 1985), and even the angiosperm family Pandanaceae (Liliopsida; Meeuse, 1961). As a consequence, the relationships of the group have been regarded as enigmatic (e.g., Andrews, 1961; Stewart, 1983). More recently, cladistic analyses of seed plants (Crane, 1985; Doyle and Donoghue, 1986) have tended to support earlier suggestions (Ehrendorfer, 1976) that the Pentoxylales are closely related to the Bennettiales and have placed both groups with the Gnetales and angiosperms in a clade of relatively derived seed plants informally termed the anthophytes (Crane, 1985; Doyle and Donoghue, 1986), which may also include *Eucommiidites*-plants (Pedersen, Crane, and Friis, 1989). The new information now available on pollen ultra-

← magnification of apertural sporoderm showing more distinct granular units of the internal sexine; note gradual thinning of sexine in the apertural region, thin sexine layer overlaying actual aperture (arrow), and more prominent nexine lamellae. TEM. Bar = 1.0 μ m. 9. Portions of two compressed pollen grains, each in the apertural region, showing lacunae at sexine/nexine interface and thinning of sexine at the aperture margin; note also the orbicules associated with the exine of a third grain in upper right of figure. TEM. Bar = 2.0 μ m. 10. Section of pollen sac wall (W) with appressed orbicules and associated lamellated tapetal membranes (arrow); note granular substructure of orbicules. TEM. Bar = 1.0 μ m. 11. High magnification of invaginated nexine in the apertural region from same pollen grain in Fig. 6. TEM. Bar = 1.0 μ m. 12. High magnification of sporoderm showing prominently invaginated exine in the sulcus; note coil-like appearance of nexine. TEM. Bar = 1.0 μ m.

TABLE 1. Comparison of *Sahnia laxiphora* pollen with other nonsaccate grains from selected extant and fossil taxa

Higher taxon	Genus/Species	Shape	Aperture type	Exine ornamentation	Organization of outer part of sporoderm	Organization of inner part of sporoderm
Pentoxylales	<i>Sahnia laxiphora</i>	Ovoid	Monosulcate	Psilate	Two layered granular/homogeneous	Faintly lamellate
Incertae sedis ^{a,b}	<i>Cycadopites</i>	Ovoid	Monosulcate	Psilate	?	?
Incertae sedis ^c	<i>Monosulcites</i> sp. 1	Ovoid	Monosulcate	Psilate	Single layer faintly granular to homogeneous	Faintly lamellate
Incertae sedis ^c	<i>Eucommiidites</i> sp. 2	Ovoid	Monosulcate with two additional lateral furrows	Psilate	Three layered homogeneous/granular/homogeneous	Lamellate
Incertae sedis ^d	<i>Eucommiidites</i> pollen from <i>Erdtmanitheca texensis</i>	Ovoid	Monosulcate with two additional lateral furrows	Psilate with occasional large granules on the proximal surface	Two layered granular/homogeneous	Lamellate
Incertae sedis ^d	<i>Eucommiidites</i> pollen from <i>Erdtmanispermum balticum</i>	Ovoid	Monosulcate with two additional lateral furrows	Punctate	Three layered homogeneous/granular/homogeneous	Lamellate
Bennettitales ^{e,f}	<i>Cycadeoidea dacotensis</i>	Ovoid	Monosulcate	Punctate, scabrate	Two layered granular/homogeneous	Nonlamellate
Bennettitales ^g	<i>Leguminanthus siliquosus</i>	Ovoid	Monosulcate	Psilate	Three layered homogeneous/granular/homogeneous	Faintly lamellate
Gnetales ^c	<i>Ephedripites</i> sp. 1	Ovoid, plicate	Monosulcate	Psilate	Three layered homogeneous/granular/homogeneous	Faintly lamellate
Gnetales ^{h,i,j,k}	<i>Ephedra</i>	Ovoid, plicate	Inaperturate	Psilate	Two layered granular/homogeneous	Lamellate
Gnetales ^{h,i,j,k}	<i>Welwitschia</i>	Ovoid, plicate	Monosulcate	Psilate	Two layered granular/homogeneous	Lamellate
Angiospermae ^s	<i>Lethomasites fossulatus</i>	Ovoid	Monosulcate	Foveolate, fossulate	Three layered very thin homogeneous/granular/homogeneous	Absent
Angiospermae ^l	<i>Pandanus</i>	Spheroidal, ovoid	Monoporate, rarely pseudocolpate	Typically echinate, occasionally psilate, finely granulate or rugulate	?	?

TABLE 1. Continued

Higher taxon	Genus/Species	Shape	Aperture type	Exine ornamentation	Organization of outer part of sporoderm	Organization of inner part of sporoderm
Cycadales ^{m,n,o,p,q,r}	Extant and fossil genera	Ovoid	Monosulcate	Psilate, foveolate, fossulate, rugulate	Two layered alveolate/homogeneous	Lamellate
Ginkgoales ^{p,q}	<i>Ginkgo biloba</i>	Ovoid	Monosulcate	Rugulate, verrucate	Three layered homogeneous/alveolate/homogeneous	Lamellate
Coniferales ^{s,t}	<i>Araucaria, Agathis</i>	Spheroidal, ovoid	Inaperturate	Scabrate, finely papillose	Irregularly granular throughout	Lamellate

^a Sah and Jain, 1964.

^b Kedves, 1985.

^c Trevisan, 1980.

^d Pedersen, Crane, and Friis, 1989; see also Doyle, Van Campo, and Lugardon, 1975.

^e Taylor, 1973.

^f J. M. Osborn, unpublished data.

^g Ward, Doyle, and Hotton, 1989.

^h Gullvåg, 1966.

ⁱ Van Campo and Lugardon, 1973.

^j Kedves, 1987.

^k Hesse, 1984.

^l Jarzen, 1983.

^m Dehgan and Dehgan, 1988.

ⁿ Audran and Masure, 1976.

^o Audran and Masure, 1977.

^p Audran and Masure, 1978.

^q Audran, 1987.

^r Hill, 1990.

^s Pocknall, 1981.

^t Ueno, 1959.

structure in the Pentoxylales, and the comparisons presented above, broadly support this systematic hypothesis. Further resolution of relationships of the Pentoxylales will hinge on the clarification of other aspects of the reproductive structure and biology of this enigmatic, but important group of Mesozoic seed plants.

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