

POLLEN MORPHOLOGY AND ULTRASTRUCTURE OF THE BENNETTITALES: IN SITU POLLEN OF *CYCADEOIDEA*¹

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The micromorphology and ultrastructure of in situ pollen from *Cycadeoidea dacotensis* are described from permineralized specimens collected from the Lower Cretaceous of North America. Pollen grains are ovoid and relatively small, averaging 25 μm in length and 12 μm in width. Grains are monosulcate with the exine typically invaginated in apertural regions. Exine ornamentation ranges from punctate to psilate. The exine averages 0.73 μm in thickness and is composed of a light-staining sexine and a dark-staining nexine. The sexine consists of a thin, homogeneous tectum, typically with a well-defined inner boundary, and a thicker granular infratectum. The infratectal granules are relatively uniform in size, however, variation occurs in the arrangement of granules. In some grains, the sexine appears homogeneous because there is little lacunal space between the individual granules. The granular infratectum is in direct contact with the underlying nexine. The nexine is uniform in thickness in both apertural and nonapertural regions, and it lacks lamellae throughout. Pollen morphology and ultrastructure are compared with those of the bennettitalean genus *Leguminanthus* and the dispersed genus *Monosulcites*. In addition, the fine structure of *Cycadeoidea* pollen is compared to that of the gymnosperm groups with which the Bennettitales are regarded to be most closely related, including Gnetales, Pentoxylales, and *Eucommiidites*-type pollen-producing plants.

In recent years it has become increasingly clear that the Bennettitales are far more taxonomically diverse than previously thought (see Crane, 1986; Taylor and Taylor, 1993). The group is best known, however, from silicified trunks with in situ reproductive organs (*Cycadeoidea* and *Monanthesia*) from the Lower Cretaceous of North America, as well as a variety of compression-impression foliage specimens (e.g., *Pterophyllum*, *Ptilophyllum*, *Zamites*) wide-ranging in both stratigraphic age and geographic occurrence. Phylogenetically, the Bennettitales are extremely important, because the group has been allied with several orders of "higher" seed plants, including Cycadales, Gnetales, and angiosperms. However, the suggested affinities with Cycadales are generally dismissed as superficial, and the two groups are now thought to be phylogenetically more disparate (see Crane, 1988 and references therein). Cladistic analyses, on the other hand, have supported the proposed relationship among Bennettitales, Gnetales, and angiosperms, and also linked these three groups with the Pentoxylales in a single, highly derived clade ("anthophytes"; Crane, 1985; Doyle and Donoghue, 1986).

Bennettitalean reproductive organs are relatively diverse morphologically, with both monosporangiate and bisporangiate forms recognized. The best known pollen-bearing organs are those of Jurassic and Cretaceous specimens; monosporangiate forms include *Weltrichia* spp.

(e.g., Sitholey and Bose, 1953, 1971; Harris, 1969; Delevoryas, 1991), while bisporangiate reproductive organs are known in *Cycadeoidea* spp. (e.g., Wieland, 1906, 1916; Delevoryas, 1963, 1965, 1968; Crepet, 1972, 1974), *Williamsoniella* spp. (e.g., Thomas, 1915; Harris, 1969; [= *Wielandiella* spp., see Watson and Sincock, 1992]), and *Amarjolia dactylota* (Bose, 1966; Sitholey and Bose, 1971; Bose, Banerji, and Pal, 1984). These fossils consist of several dorsiventrally flattened, often pinnate, microsporophylls that are attached in a whorl to a receptacle. Microsporophylls may be either fused basally into a distinct cup or attached singly around ovulate parts, with well-defined adaxial synangia containing a variable number of pollen sacs (see Crane, 1986).

Triassic pollen organs attributed to this group are principally known from disarticulated microsporophylls that differ morphologically from those of Jurassic and Cretaceous specimens. Triassic microsporophylls appear to have been arranged in a helical pattern with the pollen sacs borne individually, rather than fused into synangia (see Crane, 1986). Several of these putative bennettitalean microsporophylls include: *Leguminanthus siliquosus* (Kräusel and Schaarschmidt, 1966), *Haitingeria krasseri* (Kräusel, 1949), *Leuthardtia ovalis* (Kräusel and Schaarschmidt, 1966), and *Bennettistemon amblum*, *B. bursigerum*, and *B. ovatum* (Harris, 1932). At least one species of *Bennettistemon*—*B. valdensis* (Edwards, 1921; see also Watson and Sincock, 1992)—is also known to extend into the Lower Cretaceous. Crane (1986, 1988) has suggested that helical phyllotaxy and nonsynangiate pollen sacs, exhibited by Triassic pollen organs, are pleiomorphic features within the group.

Relatively few studies have examined bennettitalean pollen beyond the description of grains as seen in transmitted light (e.g., Van Konijnenburg-van Cittert, 1971), and the majority of these have been illustrated in the original works on the aforementioned pollen organs. Pollen is not known, however, from several *Weltrichia* species, including *W. singhii*, *W. polyandra*, and *W. santal-*

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ensis from the Rajmahal Hills, India (Sitholey and Bose, 1953, 1971), *W. ayuquilana* and *W. microdigitata* from Oaxaca, Mexico (Delevoryas, 1991), nor from *Weltrichia* sp. from the Wealden of England (Watson and Sincock, 1992). Bennettitalean pollen is typically described as small, ovoid, with a single, longitudinally oriented sulcus. By contrast, Harris (1974) described the pollen of *Williamsoniella lignieri* as circular in outline and monoporate. This study was also significant because it addressed, among a number of effects, the morphological implications of compression and tension on fossil pollen (Harris, 1974).

Significantly fewer grains are known at the ultrastructural and micromorphological levels. Two published investigations employed both scanning electron and transmission electron microscopy (SEM and TEM) in the examination of bennettitalean pollen (Taylor, 1973; Ward, Doyle, and Hotton, 1989), whereas only SEM was used to study the surface features of *Bennettistemon valdensis* pollen (Watson and Sincock, 1992). Taylor (1973) examined grains of *Cycadeoidea dacotensis* and demonstrated two different sporoderm layers based on stain affinity, but was unable to ascertain information about sexine and nexine infrastructure. Taylor did, however, refute early suggestions (Wieland, 1906) of cellular microgametophytes within *C. dacotensis* pollen by documenting that such features represented external folds in the exine. Since Taylor's (1973) study, the sporoderm of *Cycadeoidea* pollen has typically been characterized as homogeneous (e.g., Zavada, 1991). Interestingly, the pollen wall of *Williamsoniella* has also been regarded as lacking ultrastructural detail (W. L. Crepet [L. H. Bailey Hortorium, Cornell University], personal communication). On the other hand, pollen of the Triassic-dispersed microsporophyll *Leguminanthus siliquosus* has been reported as having a tectate-granular sexine and a faintly lamellate nexine (Ward, Doyle, and Hotton, 1989).

In the present investigation, previous observations on the fine structure and micromorphology of in situ pollen from *Cycadeoidea dacotensis* are clarified and expanded. Information on exine architecture is compared with that of other bennettitalean taxa known at the ultrastructural level, and addressed with respect to its phylogenetic implications.

MATERIALS AND METHODS

North American specimens of *Cycadeoidea* spp. range in age from Upper Triassic to Lower Cretaceous, and have been collected from a variety of localities; however, several Lower Cretaceous sites in the Black Hills of South Dakota and Wyoming have yielded the majority of trunks (see Wieland, 1906 and Crepet, 1974 for historical synopses and locality details). The pollen grains described in this paper were isolated from specimens of *Cycadeoidea dacotensis* (Trunk 213) housed in the Paleobotanical Collections of the Peabody Museum of Natural History, Yale University (New Haven, CT). Additional pollen from the same specimens studied by Taylor (1973) was reexamined; these fossils are housed in the Paleobotanical Collections of The Ohio State University. Hundreds of sectioned trunk pieces were examined with reflected light in order to identify appropriate specimens for palynological study. Relatively few *Cycadeoidea* trunks were found with

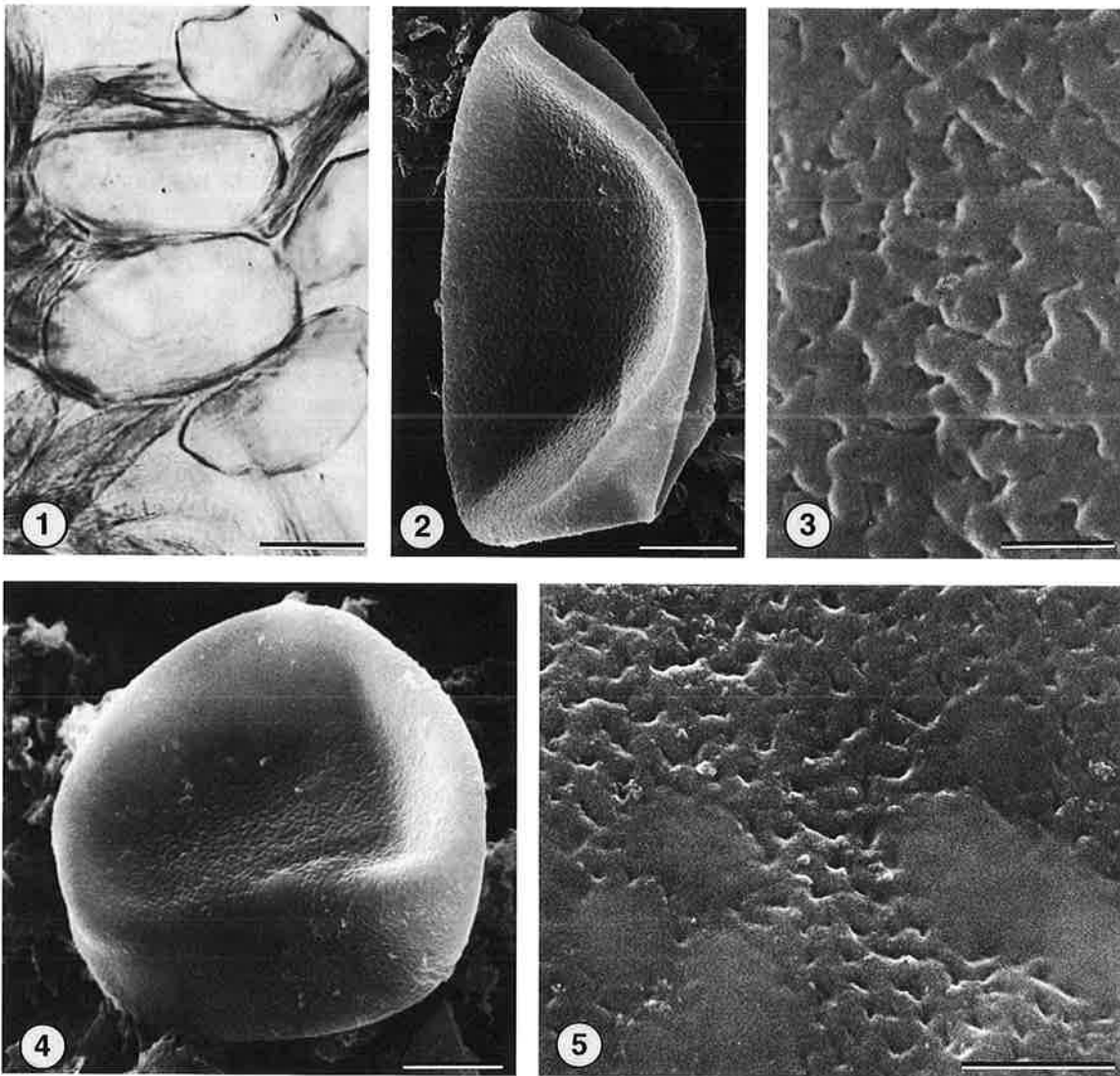
cones bearing microsporangiata organs (i.e., in a bisporangiata, or mature, developmental stage), an observation also previously made by Crepet (personal communication).

Light micrographs of pollen illustrated here were photographed from G. R. Wieland's (GW; 1906, 1916) original thin sections; these are housed along with the sectioned trunk pieces in the Collections of the Yale Peabody Museum (YPM). For electron microscopy, in situ pollen was isolated from cones by building elevated wax wells directly around synangia on the surfaces of the silicified trunk slabs. Grains were then pipette-macerated using 48% hydrofluoric acid and washed several times with distilled water. For SEM, grains were pipetted directly onto polished aluminum stubs, sputter-coated with gold-palladium, and viewed on Hitachi S-500 and JEOL JSM-840 scanning electron microscopes at accelerating voltages of 15–20 kV. Pollen for TEM was pipetted onto cellulose filters under suction; filters were then coated on both sides with agar. The agar-embedded filters were subsequently dehydrated in a graded ethanol series, transferred to 100% acetone to dissolve the filters, gradually infiltrated with Spurr low viscosity epoxy resin, and flat-embedded in shallow aluminum pans. Individual blocks overlaying embedded pollen grains were then cut from the resin disks in order to obtain specific grains in desired orientations. Ultrathin sections were cut with a diamond knife, collected on uncoated slot grids, and dried onto formvar support films (Rowley and Moran, 1975). Grids were stained with 1% potassium permanganate (3–12 min), 1% uranyl acetate (6–12 min), and lead citrate (3–6 min; Venable and Coggeshall, 1965), and images were recorded using a Zeiss EM-10 transmission electron microscope at 60–80 kV.

RESULTS

Pollen grains are typically ovoid, averaging 25 μm in length and 12 μm in width (Figs. 1, 2). A few spheroidal grains have also been identified (Fig. 4). Surface sculpturing ranges from punctate to scabrate; some also appear psilate. Although the majority of grains examined were entirely punctate (Figs. 2, 3), several showed punctate ornamentation with psilate "islands" (Fig. 5), while others were more prominently psilate. Ultrathin sections, as well as observations in transmitted light, indicate that grains are monosulcate (Figs. 6, 15). The surface morphology of the apertural membrane is more difficult to determine when observing pollen with SEM because grains are typically highly invaginated, with prominent folds present in the apertural region (Figs. 2, 12; see also Figs. 13, 14).

The exine is two-layered, with individual layers delimited from one another by different stain affinities (Figs. 6–11). The overall exine averages 0.73 μm in thickness, and is composed of an outer sexine that generally stains lightly throughout and an inner, dark-staining nexine (Figs. 6–9). The sexine averages 0.50 μm in thickness and is typically 2.2 times thicker than the underlying nexine. Ultrastructurally, the sexine has a stratified architecture consisting of two distinct zones (Figs. 7, 9). The internal stratum (= infratectum) is granular and averages 0.36 μm in thickness. Granules are relatively uniform in size, averaging 0.06 μm in diam, although variation occurs in the



Figs. 1–5. *Cycadeoidea dacotensis*. 1. Several in situ pollen grains. GW#107; YPM#5084. Bar = 20 μm . 2. Slightly folded grain showing ovoid shape and punctate ornament. Bar = 5 μm . 3. Detail of pollen surface showing punctate ornamentation. Bar = 1 μm . 4. Slightly compressed grain showing anomalous spherical shape. Bar = 5 μm . 5. Exine surface showing several psilate regions within the punctate sculpture. Bar = 2 μm .

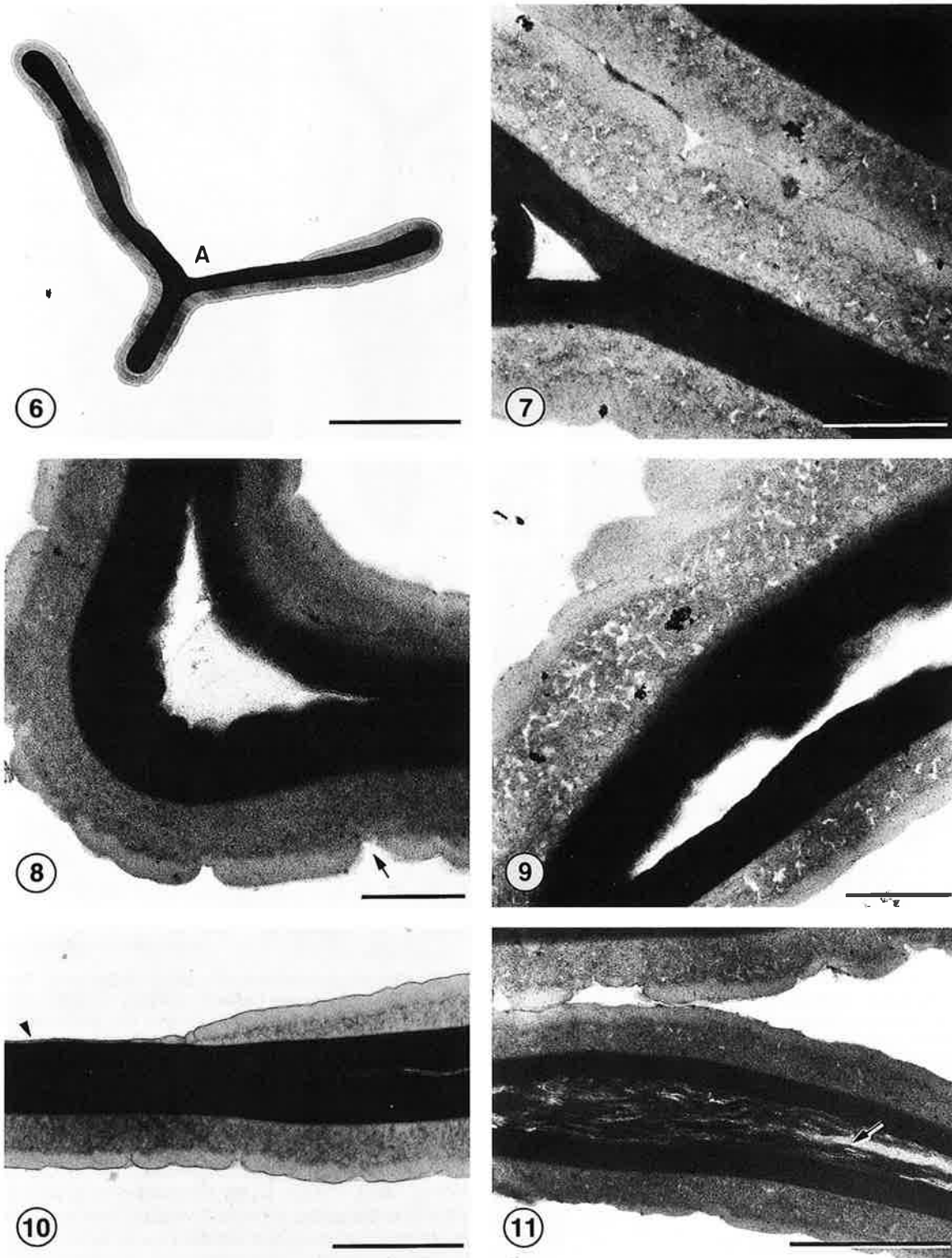
density of individual granules (Figs. 7, 9). In most grains, granule packing is relatively regular with a small amount of lacunal space between granules (Figs. 7, 9). However, some grains show less space and tighter granule packing, that results in the infratectum superficially appearing homogeneous (Figs. 8, 10). The external sexine layer (= tectum) is homogeneous and stains slightly lighter than the granular infratectum (Figs. 7–10). The tectum averages 0.14 μm in thickness and may or may not be continuous over the granular layer (Figs. 7, 8). The variability observed in surface sculpturing (i.e., psilate to punctate) is the result of structural variation of the tectum (i.e., degree of continuity). In grains, or portions of grains, that are psilate, the homogeneous tectum is entirely continuous over the granular infratectum (Fig. 8), while in scabrate and punctate grains, or exine regions, the tectum shows varying degrees of thinning (Figs. 7, 8, 11).

The nexine averages 0.23 μm in thickness and appears more dense than does the sexine (Figs. 6–11). Well-defined

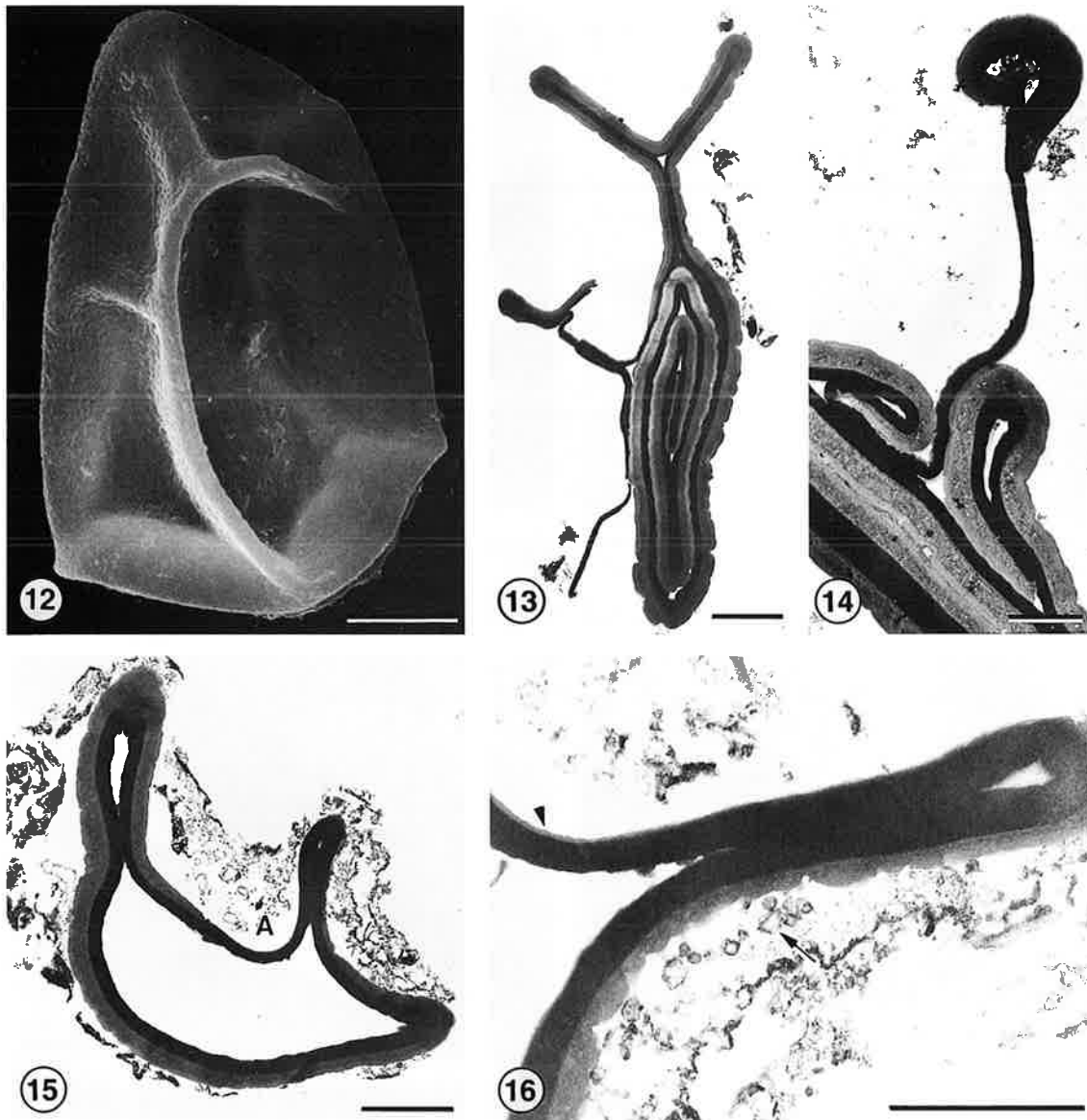
nexine lamellae have not been identified (Figs. 7–9). In some grains, however, several lamellated structures are present within the grain lumen and superficially resemble inner nexine lamellae (Fig. 11).

The apertural region is uniform in ultrastructure. A thin sexine layer, notably lacking a granular zone, overlies the dark-staining nexine layer in apertural regions (Figs. 10, 16). This is the result of a gradual, lateral thinning of the overall sexine in nonapertural regions at the margins of the sulcus (Figs. 6, 10, 16). Specifically, the granular infratectum gradually thins to a point where it becomes absent, while the homogeneous tectum remains relatively consistent in thickness and then abruptly decreases in thickness near the margins of the aperture (Figs. 6, 10). A thin layer of the tectum overlies the apertural membrane. The apertural nexine layer is similar to that of nonapertural regions regarding both thickness and in the absence of lamellae (Figs. 6, 10, 15, 16).

Definitive orbicules and resistant tapetal membranes



Figs. 6–11. *Cycadeoidea dacotensis*. **6.** Transverse section through a pollen grain showing overall ultrastructure and lightly stained sexine and darkly stained nexine; note the thinning of the sexine over the aperture (A). Bar = 5 μm . **7.** Transverse section through two grains showing thin, homogeneous tectum with intermittent thin areas corresponding to surface punctae, granular infratectum, and dark-staining nexine. Bar = 0.5 μm . **8.** Transverse section through a folded region of a grain showing exine stratification and thin regions in the tectum (arrow); note also the more densely packed granules in the infratectal layer. Bar = 0.5 μm . **9.** Oblique section through a grain showing a homogeneous tectum and well-defined infratectal granules; note that the granules are in direct contact with the dark-staining nexine. Bar = 0.5 μm . **10.** Detail of the apertural region from the same grain illustrated in Fig. 6 showing lateral thinning of the sexine and a uniformly thick nexine; note that the infratectum thins more gradually than the tectum, and that only a very thin sexinous layer is present over the apertural membrane (arrowhead). Bar = 1 μm . **11.** Transverse section through two grains showing “pseudolamellae” (arrow; see text) within the lumen of the lower grain. Note also the relatively wide, thin area in the tectum of the upper grain. Bar = 1 μm .



Figs. 12–16. *Cycadeoidea dacotensis*. 12. Folded pollen grain. Bar = 5 μm . 13. Ultrathin section through a highly folded grain. Bar = 2.5 μm . 14. Detail of a folded grain showing the ruptured exine in the apertural region; note that the exine has broken in a region occupied only by nexine. Bar = 1 μm . 15. Transverse section through a grain showing overall ultrastructure, thin exine in the apertural region (A), and associated tapetal-like material. Bar = 2 μm . 16. Detail of a different section from the same grain illustrated in Fig. 15 showing that the tapetal-like and orbicule-like (arrow) material more than likely represent maceration debris. Note also the presence of a thin, sexinous layer over the apertural membrane (arrowhead). Bar = 1 μm .

have not been identified with any of the pollen grains examined. Several grains, however, have some residual, maceration debris closely associated with exines that superficially resemble these structures (Figs. 15, 16).

DISCUSSION

One of the most distinguishing features of the *Cycadeoidea* pollen grains examined here is their excellent preservation; grain surfaces show very little damage and differentially stained sporoderm layers are distinct and easily detectable in all grains sectioned. The nexine is consistently denser (i.e., darker) relative to the overlying sexine, but distinguishable lamellae in this layer have never been observed. In fact, even structurally discernible

“faint lamellae,” that may occur in both apertural and nonapertural nexine regions of fossil gymnosperm pollen (e.g., *Sahnia* [Pentoxylales]; Osborn, Taylor, and Crane, 1991), were absent in all *Cycadeoidea* grains examined. This is interesting, especially taking into account the well-preserved nature of the pollen. In a small number of grains, however, structures are present that superficially resemble nexine lamellae. These are interpreted as either poorly preserved intine material or as some type of maceration debris. This determination is based on the fact that the grains containing these “pseudolamellae” have uniformly thick, dark-staining nexine layers present with well-defined upper and lower boundaries, and that the lamellated structures are located within the grain lumens.

Despite the fact that lamellae have not been identified,

it is possible that *Cycadeoidea* pollen does indeed have a lamellate nexine. Although multiple grains were sectioned in the present study, the circumstances under which lamellae would be detectable may have not yet been encountered. A variety of both physical and biological factors, such as preservational and developmental phenomena, are known to influence observed fine structure in fossil pollen and may preclude the detection of distinct lamellae (see Osborn and Taylor, 1994).

Such abiotic and biotic parameters may also affect sexine ultrastructure. The sexine of *Cycadeoidea* pollen is typically two-zoned, composed of a homogeneous tectum and a granular infratectum. The tectum is continuous, with the exception of intermittent thin areas that correspond with surface punctae. Within the punctae, the tectum is not completely absent, but is extremely thin. In most grains the tectum has a well-defined inner boundary and is easily delimited from the underlying granular infratectum. However, in some grains the infratectal granules are so densely packed together that the infratectum appears homogeneous throughout. Because the boundary between the infratectum and tectum in these grains is not distinct, the entire sexine appears homogeneous. The observed variation regarding infratectal fine structure (i.e., degree of granule packing) is more than likely a preservational result. The ultrastructural variability could also be due to ontogenetic effects; for example, the infratectal granules of extant *Welwitschia* (Gnetales) pollen are known to become developmentally fused, thereby giving rise to a thick, homogeneous tectum (Zavada and Gabarayeva, 1991; see Osborn and Taylor, 1994). Such an ontogenetic explanation for the infratectal variation in *Cycadeoidea* pollen is unlikely because the synangia/cones from which the grains were macerated were of the same approximate age.

The infratectum of *Cycadeoidea* pollen is further characterized by the granules being directly contiguous with the underlying, dark-staining nexine. This is significant regarding comparisons with other tectate-granular grains in which the granular infratectum may be separated from the dark-staining nexine component by a light-staining, homogeneous layer of variable thickness (foot layer sensu some authors). Nonsaccate pollen with a tectate-granular ultrastructure are synapomorphic character states of the "anthophyte" clade (e.g., Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Rothwell and Serbet, 1994). In addition to Bennettitales, Gnetales, Pentoxylales, and angiosperms, this clade may also include Mesozoic gymnosperms that produced *Eucommiidites*-type pollen (Pedersen, Crane, and Friis, 1989a).

Within Gnetales, all three extant genera (*Ephedra*, *Gnetum*, and *Welwitschia*; see Kurmann, 1992 and references therein) as well as the dispersed Lower Cretaceous palynomorph *Ephedripites* (Trevisan, 1980) are reported to have a thin, light-staining "foot layer" present. However, in another dispersed gnetalean palynomorph from the Lower Cretaceous, *Equisetosporites*, a light-staining nexine component is lacking (Osborn, Taylor, and de Lima, 1993). Within Pentoxylales, pollen of *Sahnia laxiphora* has the infratectal granules in direct contact with the dark-staining nexine layer (Osborn, Taylor, and Crane, 1991), like those of *Cycadeoidea* pollen. For *Eucommiidites* pollen-producing plants, infratectal variation exists among the var-

ious dispersed and in situ grains that have been ultrastructurally described, with a light-staining "foot layer" absent in some (*Eucommiidites* sp., Doyle, Van Campo, and Lugardon, 1975; *Eucommiidites* sp. 1, Trevisan, 1980; *Erdtmanitheca texensis*, Pedersen, Crane, and Friis, 1989a) and present in others (*Eucommiidites* sp. 2, Trevisan, 1980; *Erdtmanispermum balticum*, Pedersen, Crane, and Friis, 1989a).

Perhaps a more salient comparison is one between *Cycadeoidea* pollen and the only other cycadeoid grain that has been examined at the ultrastructural level, *Leguminanthus siliquosus* (Ward, Doyle, and Hotton, 1989). Pollen of *Leguminanthus* is ovoid, relatively small, averaging 23 μm in length and 13 μm in width, monosulcate, and has a psilate surface. The exine averages 0.70 μm in thickness, and consists of a lightly stained sexine and a darkly stained, faintly lamellate nexine. The sexine is also composed of a homogeneous tectum and a granular infratectum; however, the granules are larger in diameter and more densely packed than those in *Cycadeoidea*. Ward, Doyle, and Hotton (1989) also report that a homogeneous foot layer, resulting from the fusion of basal granules, overlies the darkly stained nexine layer. Moreover, in comparison with *Cycadeoidea*, the tectum of *Leguminanthus* pollen is thicker and more weakly defined in that it grades into the underlying granular infratectum.

In addition to *Leguminanthus*, Ward, Doyle, and Hotton (1989) suggested that some grains assigned to the dispersed palynomorph genus *Monosulcites* may have their affinities within the Bennettitales. Furthermore, monosulcate pollen found within the micropylar tubes of the Triassic bennettitalean ovules *Vardeklœftia* are reported to be similar to *Monosulcites minimus* (Pedersen, Crane, and Friis, 1989b). Two investigations have reported fine structural data for *Monosulcites*.

Lower Cretaceous grains of *Monosulcites* were described as ovoid with somewhat pointed ends, having a single, slightly folded aperture extending almost the entire length of each grain, and averaging $47 \times 25 \mu\text{m}$ in size (*Monosulcites* sp. 1; Trevisan, 1980). Trevisan (1980) reported these grains as psilate and having a thick (1.5–2.0 μm) exine, consisting of two principal layers. The inner layer (nexine) is dark-staining, lamellate, and uniform in thickness in both apertural and nonapertural regions. The outer, light-staining layer (sexine) is five to six times thicker than the nexine and appears to consist of a thin tectum and a thick, granular infratectum. However, the individual granules are not distinct. Granules appear large and highly fused throughout the infratectum, especially in the lower region where they form a basal layer. The second study of *Monosulcites* focused on Upper Cretaceous grains (*Monosulcites* sp.; Zavada and Dilcher, 1988). This grain is circular, averaging 45–50 μm in diam, monosulcate, and has a small, irregular saccus. Proximally, the exine is described as scabrate with a homogeneous infrastructure, while distally the grain is rugulate and consists of "irregularly shaped rods or partitions" (Zavada and Dilcher, 1988, p. 670). A dark-staining, inner exine layer was not identified. In our opinion, this Upper Cretaceous species of *Monosulcites* more than likely has its affinities outside of the gymnospermous anthophyte groups. This determination is based on the large grain size and alveolar appearance of the distal, infratectal elements. The latter

character in particular is more consistent with monosulcate pollen produced by Cycadales and Ginkgoales.

When comparing *Cycadeoidea* pollen with that of *Leguminanthus* (Ward, Doyle, and Hotton, 1989) and *Monosulcites* sp. 1 (Trevisan, 1980), several ultrastructural characters are shared among all three genera. These include: two differentially staining exine layers, homogeneous tectum, granular infratectum, gradual thinning of both exine layers over the apertural membrane, and uniform thickness of the dark-staining nexine layer in both apertural and nonapertural regions. Among the three taxa, however, pollen of *Cycadeoidea* is more similar to that of *Leguminanthus* in overall size, gross exine thickness, and exine fine structure. Despite these similarities, there are distinct ultrastructural differences between the pollen of the two genera that may have phylogenetic significance. In *Cycadeoidea* pollen, the tectum could be described as finely perforate (i.e., there are thin areas that give rise to surface punctae), the tectum has a well-defined inner boundary, the infratectal granules are relatively small and uniform in diameter, the infratectal granules are directly contiguous with the dark-staining nexine layer, and nexine lamellations have not yet been identified. With the identification of these palynological features, it is tempting to polarize their character states in a phylogenetic context. However, in our opinion the phylogenetic value of several of these characters is not particularly strong. For example, the observed ultrastructure of characters such as 1) a well-defined tectum and 2) granule size is potentially affected by a variety of preservational and biological influences (see above, and Osborn and Taylor, 1994). In particular, exine infrastructure of *Cycadeoidea* pollen was initially described as homogeneous throughout (Taylor, 1973), and, taking into account the infratectal variation detected among grains in the present study, it is possible that the sporoderm could have been characterized as homogeneous again here.

Nevertheless, the present study provides the first unequivocal evidence of a granular infratectum in *Cycadeoidea* pollen, and it underscores the importance of examining serial sections from multiple grains in such investigations. Documentation of a tectate-granular exine in *Cycadeoidea* thereby strengthens the proposed relationships among Bennettitales and the other anthophyte groups. However, numerous gaps exist in the current understanding of bennettitalean pollen, as high resolution data are now available for only two in situ taxa, *Cycadeoidea* and *Leguminanthus*, that are widely separated stratigraphically. In order to bridge those gaps, continued ultrastructural examinations of pollen from other poorly known Triassic and Jurassic bennettitalean pollen organs are needed.

LITERATURE CITED

- BOSE, M. N. 1966. A petrified bennettitalean flower from the Rajmahal Hills, India. *Current Science* 35: 569–570.
- , J. BANERJI, AND P. K. PAL. 1984. *Amarjolia dactylota* (Bose) comb. nov., a bennettitalean bisexual flower from the Rajmahal Hills, India. *Palaeobotanist* 32: 217–229.
- CRANE, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden* 72: 716–793.
- . 1986. The morphology and relationships of Bennettitales. In R. A. Spicer and B. A. Thomas [eds.], *Systematic and taxonomic approaches in palaeobotany*, 163–175. Clarendon Press, Oxford.
- . 1988. Major clades and relationships in the “higher” gymnosperms. In C. B. Beck [ed.], *Origin and evolution of gymnosperms*, 218–272. Columbia University Press, New York, NY.
- CREPET, W. L. 1972. Investigations of North American cycadeoids: pollination mechanisms in *Cycadeoidea*. *American Journal of Botany* 59: 1,048–1,056.
- . 1974. Investigations of North American cycadeoids: the reproductive biology of *Cycadeoidea*. *Palaeontographica, Abteilung B, Paläophytologie* 148: 144–169.
- DELEVORIAS, T. 1963. Investigations of North American cycadeoids: cones of *Cycadeoidea*. *American Journal of Botany* 50: 45–52.
- . 1965. Investigations of North American cycadeoids: microsporangiate structures and phylogenetic implications. *Palaeobotanist* 14: 89–93.
- . 1968. Investigations of North American cycadeoids: structure, ontogeny, and phylogenetic considerations of cones of *Cycadeoidea*. *Palaeontographica, Abteilung B, Paläophytologie* 121: 122–133.
- . 1991. Investigations of North American cycadeoids: *Weltrichia* and *Williamsonia* from the Jurassic of Oaxaca, Mexico. *American Journal of Botany* 78: 177–182.
- DOYLE, J. A., AND M. J. DONOGHUE. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Botanical Review* 52: 321–431.
- , M. VAN CAMPO, AND B. LUGARDON. 1975. Observations on exine structure of *Eucommiidites* and Lower Cretaceous angiosperm pollen. *Pollen et Spores* 17: 429–486.
- EDWARDS, W. N. 1921. On a small bennettitalean flower from the Wealden of Sussex. *Annals and Magazine of Natural History, Series 9*, 7: 440–442.
- HARRIS, T. M. 1932. The fossil flora of Scoresby Sound East Greenland, Part 3, Caytoniales and Bennettitales. *Meddelelser om Grønland* 85: 4–128.
- . 1969. The Yorkshire Jurassic flora. III. Bennettitales. British Museum (Natural History), London.
- . 1974. *Williamsoniella lignieri*: its pollen and the compression of spherical pollen grains. *Palaeontology* 17: 125–148.
- KRÄUSEL, R. 1949. Koniferen und andere gymnospermen aus der Trias von Lunz, Nieder-Österreich. *Palaeontographica, Abteilung B, Paläophytologie* 89: 35–82.
- , AND F. SCHAARSCHMIDT. 1966. Die Keuperflora von Neuwelt bei Basel. IV. Pterophyllen und Taeniopteriden. *Schweizerische Paläontologische Abhandlungen* 84: 1–64.
- KURMANN, M. H. 1992. Exine stratification in extant gymnosperms: a review of published transmission electron micrographs. *Kew Bulletin* 47: 25–39.
- NIXON, K. C., W. L. CREPET, D. STEVENSON, AND E. M. FRIIS. 1994. A reevaluation of seed plant phylogeny. *Annals of the Missouri Botanical Garden* 81: 484–533.
- OSBORN, J. M., AND T. N. TAYLOR. 1994. Comparative ultrastructure of fossil gymnosperm pollen and its phylogenetic implications. In M. H. Kurmann and J. A. Doyle [eds.], *Ultrastructure of fossil spores and pollen*, 99–121. Royal Botanic Gardens, Kew.
- , AND P. R. CRANE. 1991. The ultrastructure of *Sahnia* pollen (Pentoxylales). *American Journal of Botany* 78: 1,560–1,569.
- , AND M. R. DE LIMA. 1993. The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. *Review of Palaeobotany and Palynology* 77: 171–184.
- PEDERSEN, K. R., P. R. CRANE, AND E. M. FRIIS. 1989a. Pollen organs and seeds with *Eucommiidites* pollen. *Grana* 28: 279–294.
- , AND ———. 1989b. The morphology and phylogenetic significance of *Vardekloestia* Harris (Bennettitales). *Review of Palaeobotany and Palynology* 60: 7–24.
- ROTHWELL, G. W., AND R. SERBET. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Systematic Botany* 19: 443–482.
- ROWLEY, J. C., AND D. T. MORAN. 1975. A simple procedure for mounting wrinkle-free sections on formvar-coated slot grids. *Ultramicroscopy* 1: 151–155.
- SITHOLEY, R. V., AND M. N. BOSE. 1953. *Williamsonia santalensis* sp. nov.—a male fructification from the Rajmahal Series, with remarks

- on the structure of *Onteanthus polyandra* Ganju. *Palaeobotanist* 2: 29–39.
- , AND ———. 1971. *Weltrichia santalensis* (Sitholey and Bose) and other bennettitalean male fructifications from India. *Palaeontographica, Abteilung B, Paläophytologie* 131: 151–159.
- TAYLOR, T. N. 1973. A consideration of the morphology, ultrastructure, and multicellular microgametophyte of *Cycadeoidea dacotensis* pollen. *Review of Palaeobotany and Palynology* 16: 157–164.
- , AND E. L. TAYLOR. 1993. The biology and evolution of fossil plants. Prentice-Hall, Englewood Cliffs, NJ.
- THOMAS, H. H. 1915. On *Williamsoniella*, a new type of bennettitalean flower. *Philosophical Transactions of the Royal Society of London* 207B: 113–148.
- TREVISAN, L. 1980. Ultrastructural notes and considerations on *Ephedripites*, *Eucommiidites* and *Monosulcites* pollen grains from the Lower Cretaceous sediments of southern Tuscany (Italy). *Pollen et Spores* 22: 85–132.
- VAN KONIJNENBURG-VAN CITTERT, J. H. A. 1971. *In situ* gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Botanica Neerlandica* 20: 1–97.
- VENABLE, J. H., AND R. COGGESHALL. 1965. A simplified lead citrate stain for use in electron microscopy. *Journal of Cell Biology* 25: 407.
- WARD, J. V., J. A. DOYLE, AND C. L. HOTTON. 1989. Probable granular magnoliid angiosperm pollen from the Early Cretaceous. *Pollen et Spores* 31: 113–132.
- WATSON, J., AND C. A. SINCOCK. 1992. Bennettitales of the English Wealden. Monograph of the Palaeontographical Society, London: 1–228, pls. 1–23. (Publ. No. 588, part of Vol. 145 for 1991.)
- WIELAND, G. R. 1906. American fossil cycads. Carnegie Institution of Washington (Publ. No. 34), Washington, DC.
- . 1916. American fossil cycads, vol. 2, taxonomy. Carnegie Institution of Washington (Publ. No. 34, vol. 2), Washington, DC.
- ZAVADA, M. S. 1991. Determining character polarities in pollen. In S. Blackmore and S. H. Barnes [eds.], *Pollen and spores: patterns of diversification*, 239–256. Clarendon Press, Oxford.
- , AND D. L. DILCHER. 1988. Pollen wall ultrastructure of selected dispersed monosulcate pollen from the Cenomanian, Dakota Formation, of central USA. *American Journal of Botany* 75: 669–679.
- , AND N. GABARAYEVA. 1991. Comparative pollen wall development of *Welwitschia mirabilis* and selected primitive angiosperms. *Bulletin of the Torrey Botanical Club* 118: 292–302.