

Pollen morphology and ultrastructure of the Corystospermales: permineralized in situ grains from the Triassic of Antarctica

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(Received October 6, 1992; revised and accepted June 16, 1993)

ABSTRACT

Osborn, J.M. and Taylor, T.N., 1993. Pollen morphology and ultrastructure of the Corystospermales: permineralized in situ grains from the Triassic of Antarctica. *Rev. Palaeobot. Palynol.*, 79: 205–219.

Corystosperms, represented by *Dicroidium* leaves and *Pteruchus*-like pollen organs, are major components of the Early–Middle Triassic silicified flora from the Fremouw Formation of Antarctica. The micromorphology and ultrastructure of the in situ pollen contained within these organs are described. Pollen sacs of varying ontogenetic ages have been isolated. Mature grains are monosulcate and bisaccate, with large, crescent-shaped eusacci. The exine is relatively thick in the cappa region and thins toward the distal sulcus; surface ornamentation is psilate. In medial positions of the proximal wall, the exine is homogeneous but becomes tectate-alveolate in more lateral regions of the cappa. The alveolar units extend into the sacchi forming an endoreticulum; however, the endoreticulations are discontinuous and only attach to the outer walls of the sacchi. A wedge-shaped unit, where the sacchi attach to the corpus, characterizes both the proximal and distal poles. The sulcus is broad, extends the entire width of each grain, and is longitudinally flanked by elevated lips. The structural features of these grains are discussed with respect to other fossil and extant saccate pollen. The grains are systematically compared with those of other bisaccate pollen-producing plants with which the Corystospermales have been suggested to be closely related, including Glossopteridales, Caytoniales, and angiosperms (Lactoridaceae). The permineralized in situ grains are also compared with other compressed *Pteruchus* species known at the ultrastructural level and with morphologically similar dispersed palynomorphs known from Antarctic sediments.

Introduction

The taxon Corystospermales was established in 1933 for a relatively small group of Triassic seed ferns from the Upper Umkomaas Valley, Natal, South Africa (=Corystospermaceae; Thomas, 1933). Although corystospermous plants are not known from intact specimens (i.e. organic attachment), several disarticulated form genera have been found consistently within the same sediments and exhibit morphologically similar features, such as cuticular structure. The most frequently encountered and described genera belong to *Dicroidium* (leaves), *Rhexoxylon* (wood), *Pteruchus* (pollen organs), *Alisporites* (dispersed pollen),

Pilophorosperma (megasporophylls/cupules), and *Umkomasia* (ovules/seeds).

The corystosperm pollen organ *Pteruchus* was initially described by Thomas (1933) and subsequently emended by Townrow (1962a). *Pteruchus* is radially symmetrical with microsporophylls attached either helically or alternately. Individual microsporophylls terminate in a flattened head and bear numerous, pendulous pollen sacs. Pollen sacs are uniloculate, each with a single, longitudinally-oriented dehiscence suture, and contain bisaccate pollen grains. Historically, information about this pollen organ has been gained only from compression–impression specimens (e.g. Thomas, 1933; Townrow, 1962a; Pant and Basu, 1973;

Srivastava, 1974; Anderson and Anderson, 1985). However, several permineralized pollen organs similar in gross morphology to *Pteruchus* and containing *Alisporites*-type bisaccate pollen have recently been discovered in Triassic peat deposits from Antarctica (Osborn, 1991; Yao et al., 1992). The corystospermous affinities of this pollen organ and its in situ pollen are corroborated by the contemporaneous occurrence of both disarticulated *Dicroidium* foliage (Pigg, 1990) as well as leaves attached to the stem *Kykloxylon* (Meyer-Berthaud et al., 1993). In addition, *Rhexoxylon*-type wood, with possible corystosperm affinities, has also been identified in this Antarctic flora (Taylor, 1992).

In addition to *Pteruchus* and the Antarctic *Pteruchus*-like organs, several other compressed microsporophyll taxa have been suggested to have affinities with the Corystospermales (see Crane, 1988). These include *Nidiostrobus harrisiana* (Bose and Srivastava, 1973), *Kachchhia navicula* (Bose and Banerjee, 1984), and *Pteroma thomasi* (Harris, 1964).

There are few detailed studies on corystosperm pollen. In situ grains macerated from the type *Pteruchus* compression material were initially examined in transmitted light by Thomas (1933) and Townrow (1962a,b). Grains were described as being variable in size with two sacci and a single germination furrow on the distal surface; ornamentation was reported as granular to reticulate on sacci, and variable on the corpus (Thomas, 1933; Townrow, 1962a,b). Numerous stratigraphic studies have also provided information on *spora dispersae* grains that distinctly resemble *Pteruchus* pollen. These palynomorphs are most often assigned to *Alisporites* (Daugherty) Jansonius (1971) and *Pteruchipollenites* Couper (1958). Recent palynostratigraphic studies of Triassic sediments from Antarctica have revealed a relatively diverse microflora, including *Alisporites* and *Pteruchipollenites* as primary components (Farabee et al., 1989, 1990).

Relatively few grains, however, have been studied at the micromorphological and ultrastructural levels using scanning and transmission electron microscopy (SEM and TEM). Only two investigations have focused on corystosperm pollen

using SEM and TEM, and both sets of observations come from compression material (Taylor et al., 1984; Zavada and Crepet, 1985). Taylor et al. (1984) examined in situ pollen of *Pteruchus dubius* from Middle Triassic sediments from Dinmore, Ipswich, Australia, and Zavada and Crepet (1985) evaluated in situ grains from the type material of *P. africanus*, *P. dubius*, and *P. papillatus* from the Triassic Molteno beds in the Upper Umkomaas Valley, South Africa. Both studies report exine ornamentation as psilate with artifactual pitting, and variously shaped sporopollenin units separated by irregular lacunae within the sacci. Taylor et al. (1984) found the cappa region to gradually thin near the proximal pole and to be only slightly thicker than the distal region of the corpus, but they did not describe the infrastructural nature of the cappa. Zavada and Crepet (1985), however, found the proximal wall to be homogeneous with the occasional occurrence of small lacunae.

In the present investigation, the first three-dimensionally preserved corystosperm pollen grains are examined at the fine structural and micromorphological levels. In situ pollen from permineralized *Pteruchus*-like pollen organs collected in Antarctica is described and compared with other fossil and extant saccate pollen, including previously described corystosperm pollen.

Materials and methods

Corystosperm remains were recovered within a silicified peat collected north of Fremouw Peak in the Beardmore Glacier area (84°18'S, 164°20'E, Buckley Island Quadrangle; Taylor et al., 1989), central Transantarctic Mountains, Antarctica. The peat occurs in the Upper Fremouw Formation and is interpreted as Early-Middle Triassic in age based on its palynostratigraphic record (Farabee et al., 1989, 1990) and the occurrence of the stratigraphically diagnostic vertebrates *Lystrosaurus* and *Cynognathus* (Hammer, 1990).

For light microscopy (LM), surfaces of sectioned slabs of peat bearing the *Pteruchus*-like pollen organs were etched in 48% hydrofluoric acid for 1–5 min. Etched slabs were serially peeled with cellulose acetate; peels were then mounted on

microscope slides and photographed using bright-field and Nomarski illumination. A large number of sectioned slabs contained well-preserved pollen organs (Yao et al., 1992); however, slabs/faces 10,717 Btop, 10,178 Btop and Cbot, and 10,925 Btop contained organs with copious amounts of pollen. All slabs and peels are housed in The Ohio State University Paleobotanical Collections.

For electron microscopy, additional *in situ* grains were isolated from specimens by building elevated wax wells directly over pollen sacs containing specific grains of interest (i.e. ontogenetic age, preservation). Grains were then pipet-macerated with 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 a Hitachi S-500 scanning electron microscope at an accelerating voltage of 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 with at least four acetone changes (Osborn et al., 1991), gradually infiltrated with Spurr epoxy resin, sectioned into several pieces, and embedded flat in shallow aluminum pans. Individual blocks overlaying the embedded pollen grains were then cut out in order to obtain both specific grains as well as their specific orientations for desired planes of section. Ultrathin sections were cut with a diamond knife, collected on uncoated 1 × 2 mm slot grids, and dried onto formvar support films (Rowley and Moran, 1975). Grids were triple stained with 1% potassium permanganate (2–30 min), 1% uranyl acetate (2–30 min), and lead citrate (1–15 min; Venable and Coggeshall, 1965), and images were recorded using a Zeiss EM-10 transmission electron microscope at 60–80 kV.

Results

Permineralized pollen sacs are elliptic, unilocular, and relatively small in size, ranging from 0.7 to 3.0 mm in length and from 0.44 to 0.50 mm in width (Plate I, 1–3). Each sac has a single epidermal layer composed of elongate, slightly sinuous

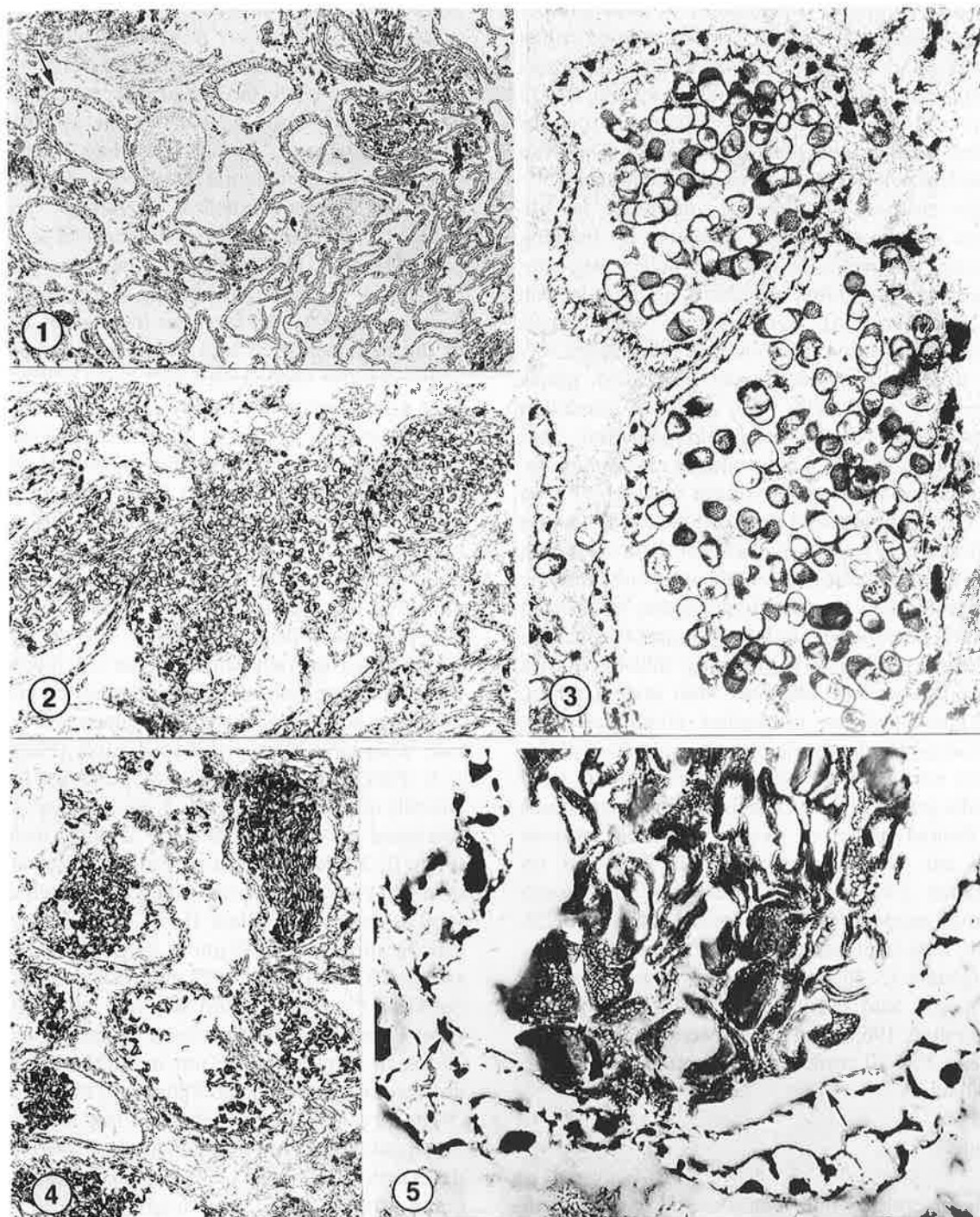
cells and larger, intercalary secretory cells that occur at irregular intervals (Plate I, 1–3). Three types of pollen sacs were recovered from the peat and are believed to represent different developmental stages. In one, the individual sacs are completely devoid of pollen and have split open at a site of dehiscence (Plate I, 1). The second type contains numerous grains that are completely dissociated from one another (Plate I, 2, 3). A third type of pollen sac, containing large numbers of densely packed grains, also occurs in the same matrix (Plate I, 4, 5). The tight packing of pollen grains is underscored by the fact that they macerate out of the permineralized sacs in distinct clumps. In addition to the single-celled wall, these pollen sacs have a thin membranous layer which occurs just inside the wall (Plate I, 5). These tapetal-like membranes have been identified in several pollen sacs and are variable in their form.

Pollen sacs with dissociated grains are interpreted as mature, while those containing aggregated pollen grains are believed to be immature, but preserved in a relatively late developmental stage (see Discussion below). As such, the two grain types are structurally similar; thus the following descriptions are restricted to the dissociated grains.

Mature pollen grains are monosulcate and bisacate with large, crescent-shaped sacchi (Plate II, 1–4; Plate IV, 1–5). Sacchi are generally found laterally attached (Plate II, 1, 3, 4); however, a few specimens have sacchi that are distally inclined (Plate II, 2). Pollen grains typically average 66 µm in length (saccus to saccus) and 49 µm in width as seen in polar view (Plate II, 1, 3). In equatorial view, grains average 30 µm in height. The corpus averages 33 µm in length, 22 µm in height (equatorial view; Plate III, 1), and 49 µm in width (polar view; Plate II, 1). Sacchi average 30 µm in length, 20 µm in height, and 36 µm in width, and have distinct endoreticulations (Plate II, 6; Plate III, 1).

The proximal wall is characterized by psilate ornamentation. Although numerous pits occur on the exine surface, these are interpreted as preservational artifacts based on the irregularity of their size, shape, and distribution (Plate II, 3, 5). In the cappa region, the exine is homogeneous and averages 1.0 µm in thickness (Plate III, 3). However, some ultrastructural variability is detect-

PLATE I



able in this region. For example, some grains show a slight degree of differential staining (Plate III, 4). This variation may also be the result of preservational phenomena. Although grains typically have homogeneous exines in the cappa region and do not show differentially stained sporoderm layers, the presence of two distinct layers (= sexine and nexine) is especially detectable in peripheral corpus positions, where the layers separate to form sacci.

The region of saccus attachment to the proximal wall is characterized by a wedge-like unit, formed by the initial separation of wall layers, which gradually dialates to form the saccus (Plate III, 1, 5–7). Morphologically, endoreticulations originate at the “tip” of the wedge-like unit (i.e. medially near the cappa), where they extend across the entire unit and make contact with both exine layers. In the more dialated regions, the endoreticulations separate with the short and discontinuous reticulations attached only to the outer exine layer, which forms the outer saccus wall (Plate III, 5–7). The size and ultrastructural nature of wedge-like units may vary depending on both the angle of saccus inclination and the equatorial positions from which ultrathin sections are cut (i.e. medial or lateral equatorial sections; Fig. 1; Plate III, 5, 6). The plane of section through a grain is also highly significant with regard to interpreting exine fine structure in the cappa region (Fig. 1). In particular, in lateral equatorial sections the wedge-like units of both sacci are elongated and make contact. Here the reticulations are continuous, extending between both exine layers across the entire proximal wall (Plate V, 1, 2). Exine fine

structure in this region of the cappa is markedly different in comparison with the homogeneous wall organization seen in medial sections (cf. Plate III, 1, 3, 4).

Sacci are large, psilate in external ornament, and have relatively thin outer walls (Plate IV, 1, 5, 6). Endoreticulations are principally attached to the outer saccus walls with spaces of 2–3 μm between each member of the reticulum (Plate III, 1; Plate IV, 2). The endoreticulations are also relatively robust, averaging 0.30 μm in width and 1.92 μm in length (Plate III, 1; Plate V, 6), and can easily be detected from an external view (i.e. LM or SEM; Plate IV, 1, 5, 6). The nexine layer that forms the saccus floor (= inner saccus wall or lateral corpus wall) is relatively thin, averaging 0.38 μm in thickness, and may bear short, discontinuous reticulations in medial grain positions (Plate III, 1, 2; Plate V, 6). However, lateral sections indicate that endoreticulations are continuous between the outer wall and floor of the saccus (Plate V, 5).

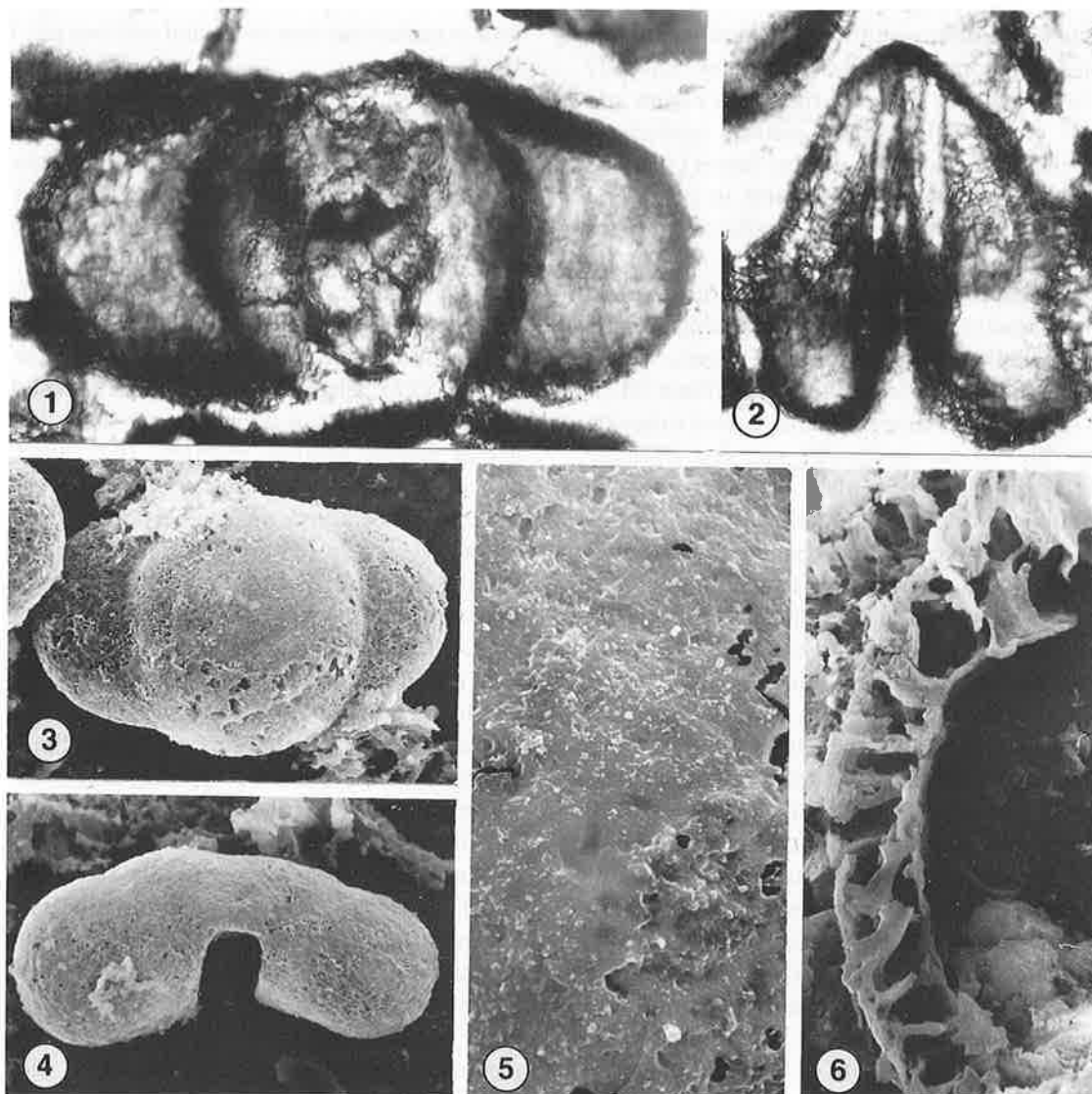
A relatively broad sulcus, averaging 9.2 μm in width and extending the entire width of each grain, characterizes the distal surface (Plate IV, 3–5). Aperture membranes are typically not well preserved (Plate IV, 5); however, when they can be identified they are thin, averaging 0.22 μm in thickness, and also have a psilate surface (Plate IV, 3, 4; Plate V, 4). Although most grains lack an aperture membrane, one diagnostic feature of all grains is the presence of elevated lips that longitudinally flank the sulcus (Plate IV, 3–5). Sacci are also attached to the corpus in distal regions by wedge-like units (Plate III, 1; Plate V,

PLATE I

Permineralized corystosperm pollen sacs. (10,717 Btop 2 \times)

1. Oblique transverse section through a pollen organ showing several dehiscent pollen sacs split open along sutures and completely devoid of grains. Other sacs containing numerous pollen grains are present in the upper right of the figure. Note also the intercalary, secretory cells in the pollen sac walls (arrow). $\times 20$.
2. Oblique, longitudinal section through several pollen sacs showing numerous in situ grains. $\times 32$.
3. Oblique, transverse section through two pollen sacs containing dissociated, bisaccate grains. Note the single-celled pollen sac wall. $\times 110$.
4. Oblique, longitudinal section through several pollen sacs containing numerous, tightly aggregated pollen grains. $\times 43$.
5. Detail of the pollen sac illustrated in the upper right of 4, showing single layered wall, resistant tapetal-like membrane (arrows), and tightly aggregated grains. Note the presence of endoreticulations within pollen grain sacci. $\times 313$.

PLATE II



In situ corytosperm pollen.

1. Proximal view of grain showing rounded corpus and laterally attached sacci. $\times 1100$.
2. Equatorial view of grain showing distally inclined sacci. $\times 1100$.
3. Proximal view of grain. $\times 800$.
4. Equatorial view of grain showing broad, distal sulcus. $\times 800$.
5. Detail of cappa region showing psilate surface ornamentation. Note the small pits which are interpreted as artifacts of preservation. $\times 4000$.
6. Fractured portion of the outer saccus wall showing endoreticulations. $\times 3500$.

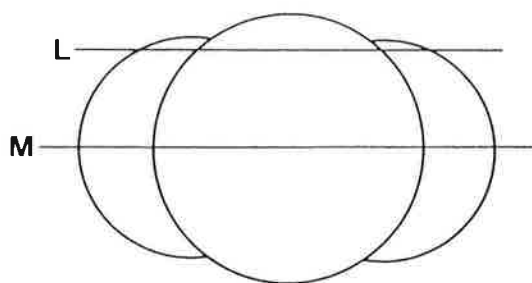


Fig. 1. Proximal view of pollen grain showing approximate planes through which medial (*M*) and lateral (*L*) equatorial sections have been cut.

3). These distal units are similar in fine structure to those of the proximal wall with regard to both the extension and separation of endoreticulations; however, distal units are less variable ultrastructurally in equatorial positions (i.e. they do not gradually taper and fuse), because the elongate sulcus extends the entire width of each grain and prevents overlap of sacci.

Discussion

Structural features of the exine

One of the most notable aspects of pollen wall ultrastructure in these corytosperm grains is the absence of two differentially staining exine layers. Several interpretations for this condition can be suggested. First, components of the nexine and sexine wall layers do not show varying affinities for heavy metal stains in these grains, and thus grade into one another resulting in an ultrastructurally homogeneous exine throughout (i.e. as seen in medial sections). This postulate is extremely unlikely for several reasons. For example, differentially stained exine layers occur commonly in the majority of fossil and extant pollen grains that have been either double or triple stained following standard procedures. Secondly, a light staining sexine and dark staining nexine have also been observed in pollen of *Pteruchus africanus*, *P. dubius*, and *P. papillatus* (Zavada and Crepet, 1985).

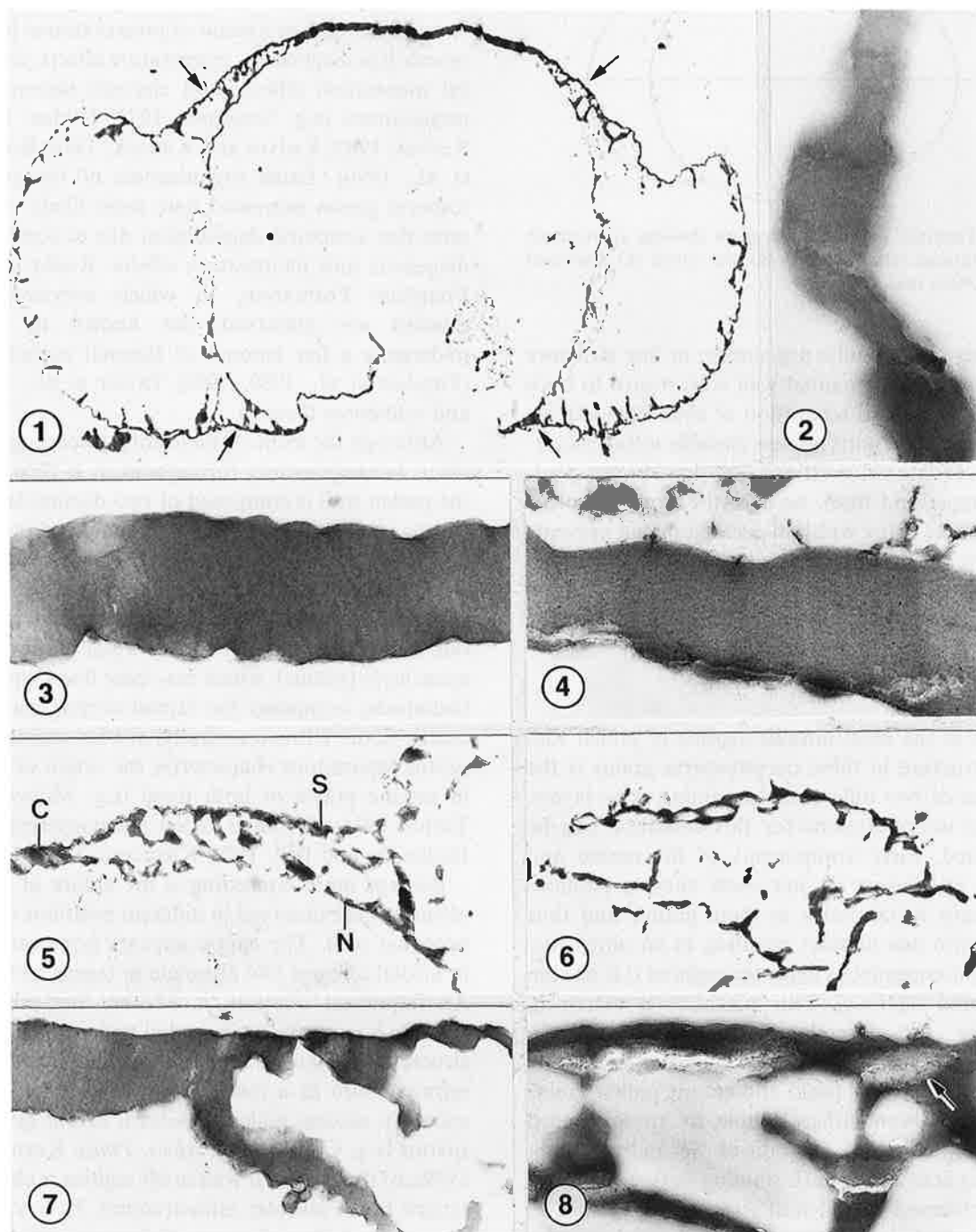
A more plausible explanation for the homogeneous exine is that the grains have undergone some type of structural modification, and the absence of

two distinct layers is artifactual. Exine ultrastructure of both fossil and extant pollen may be variously altered as a result of preservational phenomena (i.e. diagenesis), temperature effects, chemical maceration effects, and electron microscopy preparations (e.g. Sengupta, 1977; Niklas, 1980; Kedves, 1985; Kedves and Kincsek, 1989; Rowley et al., 1990). Exine organization of the corytosperm grains examined here most likely represents fine structural degradation due to combined diagenetic and temperature effects. Rocks in the Fremouw Formation, in which corytosperm remains are preserved, are known to have undergone a fair amount of thermal maturation (Farabee et al., 1989, 1990; Taylor et al., 1989, and references therein).

Although the exine of these corytosperm grains stains homogeneously throughout, it is clear that the pollen wall is composed of two distinct layers. This is evident in both proximal and distal regions of the corpus where the exine separates to form sacci. The external exine layer (sexine) splits off to compose the outer saccus wall and has discontinuous endoreticulations attached, while the internal exine layer (nexine), which may bear fewer endoreticulations, composes the lateral corpus wall, or saccus floor. Ultrastructurally, similar sexine and nexine separations characterize the origin of sacci in saccate pollen of both fossil (e.g. Millay and Taylor, 1974, 1976) and extant gymnosperms (e.g. Dickinson and Bell, 1970; Kurmann, 1989a,b).

Perhaps more interesting is the nature of exine ultrastructure observed in different positions of the proximal wall. The cappa appears homogeneous in medial sections and alveolate in lateral sections. An important question is whether the exine is actually homogeneous in medial regions, or is also structurally alveolate here but has lost its alveolar infrastructure as a result of preservational influences. In saccate pollen of several extant gymnosperms (e.g. Coniferales - *Abies*, *Pinus*; Kurmann, 1989a,b) the proximal wall in all regions is characterized by an alveolar infrastructure. However, in the saccate pollen of several Paleozoic seed plants (e.g. Callistophytales - *Idanotkekion* [*Vesicaspora*]; Cordaitales - *Cordaianthus* [*Sullisaccites*] and *Gothania* [*Felixipollenites*]) the alveolate structure does not extend entirely over the corpus in the

PLATE III



proximal wall, but rather is restricted to lateral positions where sacci overlap in attachment (Millay and Taylor, 1974). It should be noted, however, that sexine organization is known to gradually lose resolution with regard to its infrastructure in pollen grains that have undergone increasingly more thermal maturation (as detected by relative darkness of grains; Zavada, pers. commun.). The corystosperm grains evaluated here were in fact quite dark in color, and more than likely have lost some fine structural information. We believe, however, that these grains have not been diagenetically altered to the degree of completely losing a possible alveolar infrastructure, but originally lacked this type of organization in the medial cappa region. It is interesting to note that the cappa region of compressed *Pteruchus* pollen also shows a homogeneous organization, with a few small lacunae (Zavada and Crepet, 1985).

In addition to providing detailed data about the corpus wall, the permineralized grains are especially important with regard to new information gained about corystosperm sacci. Saccus organization of *Pteruchus* pollen has received a significant amount of attention in previous descriptions. The majority of this attention has been focused on the nature of the endoreticulations (meshes sensu Townrow, 1962b; see Taylor et al., 1984). Based on observations in transmitted light, ornamentation of the saccus has been variously described as completely psilate ranging to highly reticulate (Thomas, 1933; Townrow, 1962a,b; Pant and Basu, 1973). Moreover, the early literature is relatively

ambiguous as to whether sacci reticulations represent external or internal ornament. Taylor et al. (1984) clarified the internal presence of endoreticulations in Australian material of *P. dubius*; this was subsequently confirmed in the three type South African species of *Pteruchus* by Zavada and Crepet (1985). Both studies found sacci to be densely filled with endoreticulations (sporopollenin units sensu Taylor et al., 1984; infrastructural processes sensu Zavada and Crepet, 1985). Although Zavada and Crepet suggested that the endoreticulations "can be free or fused to a thin basal layer", which we interpret as the saccus floor, neither investigation was able to unequivocally document whether *Pteruchus* pollen is protosaccate or eusaccate (Scheuring, 1974) because all grains examined were extremely compressed. The permineralized grains sectioned in the present study clearly indicate that corystosperm sacci are eusaccate. Grains sectioned equatorially and through a medial plane illustrate the presence of well-defined, discontinuous endoreticulations. Interestingly, however, when grains are sectioned through a lateral equatorial plane, sacci superficially appear as though they are protosaccate. In these sections, reticulations are continuous between the floor and outer walls of the sacci, because this is where sacci are tapering to their margins and beginning to slightly overlap in their attachment to the corpus. Endoreticulations in the sacci of modern *Pinus strobus* show a similar organization in both medial and lateral regions when respective grain positions are sectioned (Taylor et al., 1987).

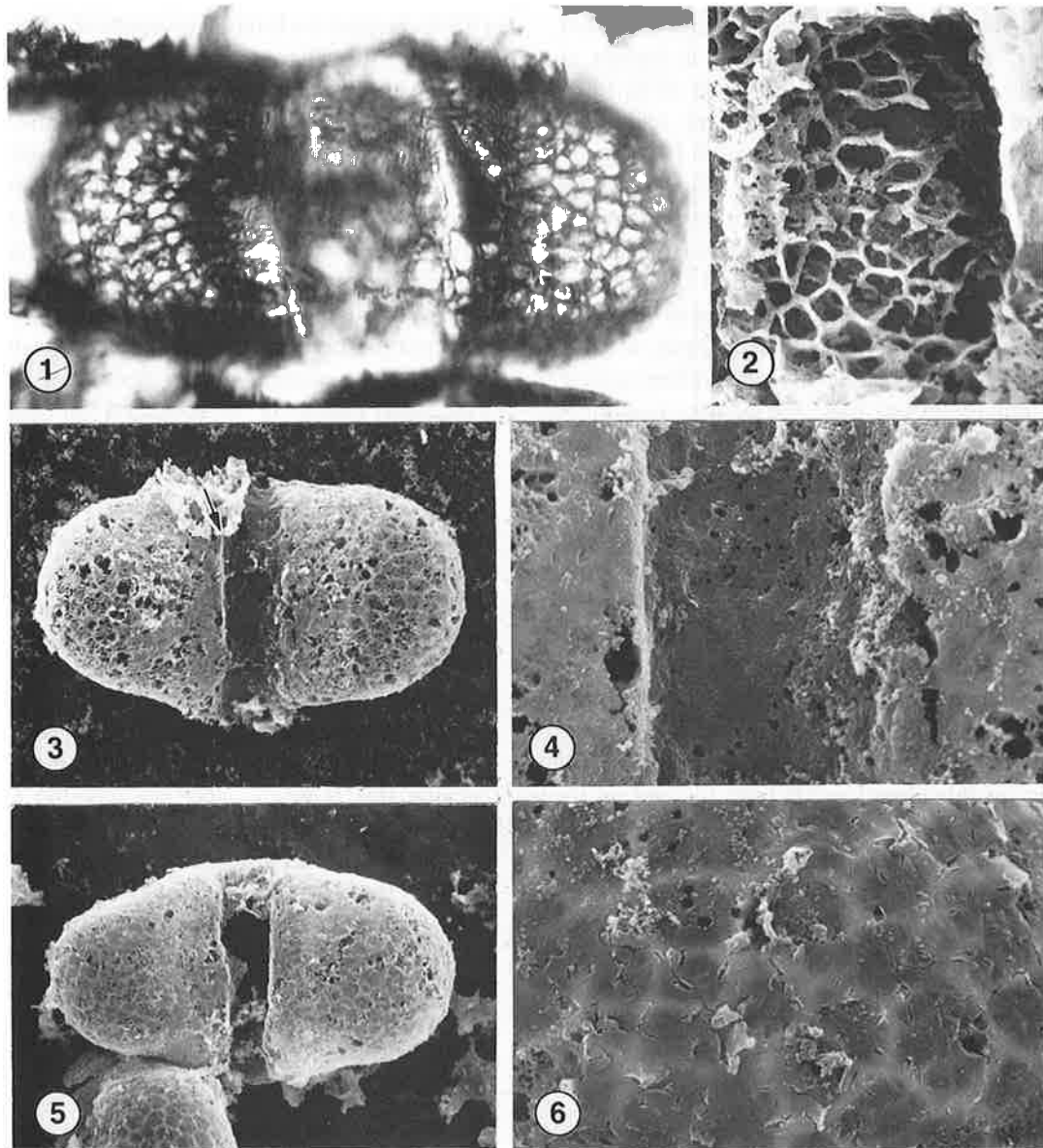
The fact that permineralized pollen sacs exhibit-

PLATE III

In situ corystosperm pollen.

1. Medial, equatorial section through a pollen grain showing overall ultrastructure. Note the homogeneous cappa wall, wedge-like units at the sites of sacci attachment (arrows), and discontinuous endoreticulations within sacci. $\times 1775$.
2. Detail of the nexine composing the lateral corpus wall (=saccus floor). $\times 20,100$.
3. Transverse section of the cappa wall from the same grain illustrated in 1, showing homogeneous organization. $\times 31,500$.
4. Oblique section of the cappa from a different grain showing slight differential staining of the wall in some regions. $\times 20,100$.
5. Wedge-like attachment of a lateral saccus showing endoreticulations extending between "upper" (=sexine, S) and "lower" (=nexine, N) wall layers. Note also the homogeneous cappa (C). $\times 5150$.
6. Wedge-like attachment of a distally inclined saccus. $\times 4150$.
7. Detail in region of saccus attachment showing homogeneous cappa wall at left, separation of wall layers, and discontinuous endoreticulations. $\times 20,100$.
8. Detail of a different wedge-like unit showing continuous endoreticulations; note diagenetic modification of the wall (arrow). $\times 20,100$.

PLATE IV



In situ corytosperm pollen.

1. Distal view of grain showing broad sulcus and laterally attached, internally ornamented sacci. $\times 1100$.
2. Internal surface of saccus showing general organization and size of the endoreticulum. $\times 2000$.
3. Distal view of grain showing intact apertural membrane and "elevated lips" (arrow) flanking the margins of the sulcus at the sites of sacci attachment. $\times 800$.
4. Detail of the sulcus in 3 showing the psilate surface of the apertural membrane with preservational pitting. $\times 3500$.
5. Distal view of grain showing ruptured apertural membrane and well-defined "lips" flanking the margins of the sulcus. $\times 800$.
6. Detail of the outer saccus wall showing psilate ornament; note also the robustness of the internal endoreticulations which are discernable from this external view. $\times 5000$.

ing different ontogenetic stages have been isolated is also interesting, and represents the first documented example of this in the Corystospermales. Pollen sacs containing completely dissociated grains are interpreted as mature, and the features of mature grains macerated from these sacs have been discussed above. Pollen sacs containing tightly-aggregated grains are interpreted as immature, but relatively close to maturity. Based on the ultrastructure and orientation of individual grains within the larger aggregates, as well as the presence of resistant membranes within pollen sacs, it is suggested that these pollen sacs were fossilized in the final stages of the "free-sporing period" of development. Evidence for this hypothesis comes from the following: (1) grains do not appear to be linked into distinct tetrads, but had apparently undergone separation and were still in very close proximity to one another; (2) exine organization of the cappa region is similar to that of mature grains in that it is homogeneous; (3) well-defined endoreticulations are easily detectable and have apparently undergone complete ontogeny; and (4) resistant membranes just inside the pollen sac walls closely resemble peritapetal membranes. All four of these features characterize the free-spore period during the ontogeny of saccate pollen in modern conifers (e.g. Kurmann, 1989a, 1990). Fewer studies, however, have addressed the developmental aspects of fossil pollen, although tapetal membranes, sometimes described along with orbicules, have been reported in several Paleozoic (Taylor, 1976a,b, 1982; Taylor and Zavada, 1986) and Mesozoic (Taylor and Alvin, 1984; Zavada and Crepet, 1986; Osborn, 1991; Osborn et al., 1991) gymnosperms.

Systematic comparisons

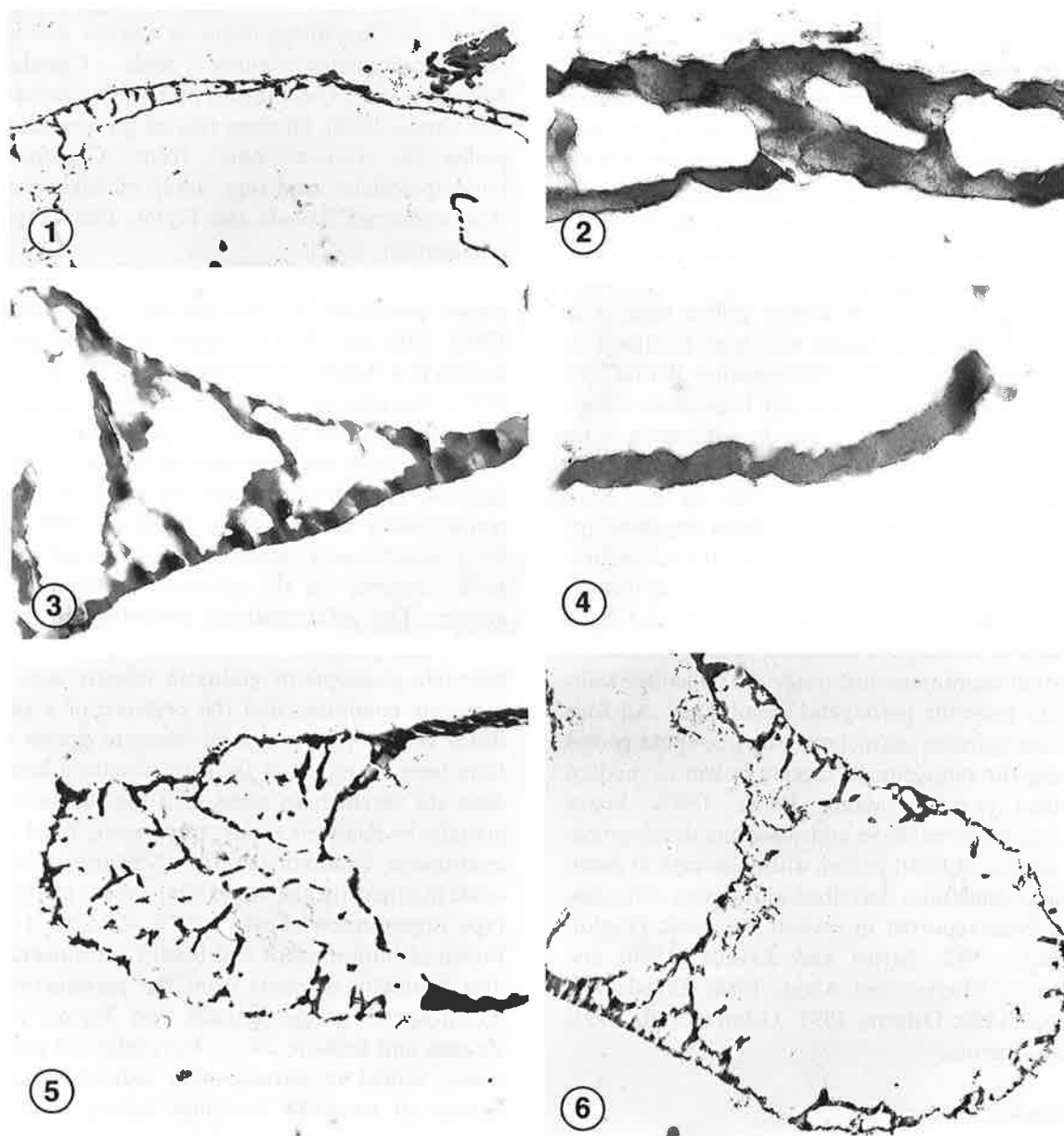
Recent phylogenetic studies of seed plants (e.g. Crane, 1985; Doyle and Donoghue, 1986) have suggested that the Corystospermales occupy a position in the sister group of an informally designated clade referred to as "anthophytes". This clade consists of Bennettitales, Pentoxylales, Gnetales, angiosperms, and perhaps plants that produced *Eucommiidites*-type pollen (Pedersen et al., 1989). Crane (1985) linked the

Corystospermales to anthophytes as their direct sister taxon, while Doyle and Donoghue (1986) placed the Corystospermales in a sister group to the anthophytes along with Cycadales, Peltaspermales, Caytoniales, and Glossopteridales (see Crane, 1988). Of these related groups, saccate pollen is known only from Caytoniales, Glossopteridales, and one family of angiosperms (Lactoridaceae; Zavada and Taylor, 1986; Zavada and Benson, 1987).

There is limited published information on the pollen produced by glossopterids (e.g. Osborn, 1991), with very few examples of in situ pollen known (e.g. Gould and Delevoryas, 1977; Zavada, 1991). The majority of data comes from dispersed grains found in association with glossopterid megafossils, or from palynostratigraphic studies. These putative glossopterid grains are relatively large, transitionally saccate (sensu Traverse, 1988), and have conspicuous longitudinally-oriented striations (taeniae) on the proximal surface of the corpus. The permineralized corystosperm grains clearly lack proximal taeniae, and only superficially resemble glossopterid grains in relative size, the bisaccate condition, and the presence of a single distal sulcus. Moreover, the taeniate grains that have been examined at the ultrastructural level to date are variable. In some taxa the taeniae may actually be relatively small "protosacci" filled with continuous endoreticulations (Scheuring, 1974), while in others the taeniae exhibit a more alveolate-type organization (Foster, 1979; Zavada, 1991). Pollen of both modern and fossil Lactoridaceae is also distinctly different from the permineralized corystosperm grains (Zavada and Taylor, 1986; Zavada and Benson, 1987). The grains are permanently united in tetrads, with individual grains having an ovoid to lenticular sulcus. Sacci are reduced in size and exine infrastructure is granular.

By comparison to glossopterid and lactoridacean pollen, the permineralized corystosperm grains more closely resemble bisaccate pollen of the Caytoniales, especially with regard to cappa ultrastructure. The infrastructural exine of *Caytonanthus* pollen is composed of sporopollenin units that can be categorized as relatively short, plate-like alveoli (Pedersen and Friis, 1986; Zavada and Crepet, 1986; Osborn, 1991). The

PLATE V



In situ corystosperm pollen.

1. Lateral, equatorial section through the cappa wall showing elongated regions of saccus attachment; note that both wedge-like units nearly fuse centrally and that endoreticulations are continuous between outer (sexine) and inner (nexine) wall layers. $\times 2060$.
2. Detail of the central cappa region from a more lateral section of the same grain illustrated in 1. $\times 20,100$.
3. Saccus attachment to the distal wall showing endoreticulations extending between both wall layers. $\times 8050$.
4. Detail of the apertural membrane. $\times 20,100$.
5. Lateral, equatorial section through a saccus showing continuous endoreticulations between the outer wall and floor of the saccus, and thereby superficially appearing "protosaccate". Note the extensive diagenetic modification of both the proximal and distal walls of the corpus at right of figure. $\times 2100$.
6. Medial, equatorial section through a saccus showing eusaccate condition with discontinuous endoreticulations attached to the outer saccus wall and the saccus floor. $\times 2600$.

most striking comparison between these grains and the permineralized corystosperm grains is that the infrastructural exine elements in *Caytonanthus* pollen also grade into a more homogeneous organization over the cappa median (Osborn, 1991). However, *Caytonanthus* pollen is markedly different in several features. By comparison, *Caytonanthus* grains are significantly smaller than the pollen of corystosperms, infrastructural elements and endoreticulations are much more robust in size, and the sacchi do not appear to attach to the corpus by distinct wedge-like units (Osborn, 1991).

Based on the above comparisons, the permineralized corystosperm grains do not unequivocally compare with any of the noted major groups, but rather appear to be unique in ultrastructure. However, comparisons with previously described in situ compression grains and *spora dispersae* grains with putative corystosperm affinities may be more useful.

The permineralized in situ grains described here are more similar in size to pollen of *Pteruchus dubius* collected from Australia (Taylor et al., 1984) relative to the South African type pollen of *Pteruchus africanus*, *P. dubius*, and *P. papillatus* (Zavada and Crepet, 1985). The Australian grains, however, do not appear to be well preserved in either the proximal or distal regions of the corpus, thereby precluding ultrastructural comparisons. On the other hand, South African *Pteruchus* pollen is similar in cappa fine structure to the permineralized grains, in that both types exhibit a homogeneous organization. Both studies of compressed *Pteruchus* pollen also report exine thinning in the cappa region; this, however, was not observed in the permineralized grains, and may represent an artifact of preservation. Exine thinning is known to be one of the first types of structural modifications seen in corroded/degraded pollen grains (Rowley et al., 1990). Another interesting similarity between the permineralized Antarctic grains and compressed pollen from the Australian specimens is the consistent occurrence of thickened, elevated lips lining the aperture margins.

The most frequently encountered dispersed grains with possible corystosperm affinities are those assigned to the form genera *Alisporites* and

Pteruchipollenites. Both genera are morphologically similar. For example, *Alisporites* is classified by such subtle differences as a slightly more rounded amb and finer endoreticulations in comparison to an ovoid shape and more robust endoreticulations in the latter (e.g. Farabee et al., 1989). In addition, *Pteruchipollenites* grains are reported to be slightly smaller, have a thinner sporoderm lacking a preformed sulcus, and exhibit greater diversity with respect to saccus endoreticulations. Perhaps more interesting are the *spora dispersae* grains described from other Triassic sediments in Antarctica (Farabee et al., 1989). Farabee et al. (1989) noted four species of *Alisporites* and one species of *Pteruchipollenites* within their samples. Of these taxa, the structurally preserved in situ grains most closely resemble *Alisporites parvus* de Jersey (1962) with regard to overall size and general morphology. Moreover, the permineralized Antarctic grains are further allied with *Alisporites*-type palynomorphs based on their relatively large sizes, the occurrence of a distinct sulcus, and similar thickenings along the aperture margins in some species of *Alisporites* (*A. australis*; Foster, 1979).

Although the permineralized in situ grains described here do not answer all of the questions concerning corystosperm pollen, they do provide new information about several important fine structural features. The importance of these specimens is underscored by the unequivocal demonstration of eusacci in this group of Mesozoic gymnosperms. Further investigations of corystosperm reproductive organs, especially fine structural studies of pollen from those microsporangiate organs suggested to be corystospermous (i.e. *Nidiostrobus*, *Kachchhia*, and *Pteroma*) will no doubt provide additional information that may be relevant in more highly resolved systematic and phylogenetic evaluations.

Acknowledgements

This investigation represents a portion of a dissertation submitted by the first author in partial fulfillment of the requirements for the Ph.D. degree from The Ohio State University. This study was supported in part by a Doctoral Dissertation

Improvement Grant from the National Science Foundation (BSR-9016397), a Student Scholarship from the American Association of Stratigraphic Palynologists, and a Grant-in-Aid of Research from Sigma Xi to JMO, and an NSF grant (DPP-9118314) to TNT.

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