The morphology and ultrastructure of *Caytonanthus*

JEFFREY M. OSBORN
Division of Science, Northeast Missouri State University, Kirksville, MO 63501, U.S.A.

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The morphology and ultrastructure of *Caytonanthus arberi* pollen organs and pollen, collected from the Middle Jurassic, Cayton Bay locality of England, are described. Pollen organs consist of flattened rachises with subopposite branched pinnae, which bear terminal synangia. The synangium is covered with a two-zoned (fibrillar and amorphous) cuticle. The locule of each pollen sac is lined with a lamellated tapetal membrane and contains numerous pollen grains and orbicules. Grains are small, monosulcate, and bisaccate. Exine ornamentation of the proximal wall is psilate, while distally the apertural membrane is scabrate. The exine is composed of a thick, lightly staining sexine and a thin, darkly staining nexine. The sexine is tectate-alveolate laterally, becoming nearly homogeneous medially. The infratectal alveolae are robust and are continuous with the endoreticular units of the sacci. Sacci are eusaccate, with endoreticulations attached only to the outer walls. Several immature grains have also been identified and indicate that the nexine is lamellate throughout and that infratectal alveolae and nexine lamellae are well developed prior to complete tectum synthesis. Saccus size and ultrastructure of *Caytonanthus* pollen are compared with those of other Late Paleozoic and Mesozoic seed ferns that produced saccate pollen (Callistophytales, Glossopteridales, Corystospermales) and found to be smaller and more extensively filled with thicker endoreticulations. Documentation of the eusaccate character state in *Caytonanthus* is also discussed regarding its phylogenetic implications.

Key words: *Caytonanthus*, Caytoniales, Mesozoic, pollen, seed fern, ultrastructure.

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L'auteur décrit la morphologie et l'ultrastructure du pollen et des organes polliniques du *Caytonanthus arberi* datant du Jurassique moyen, dans la localité de Cayton Bay en Angleterre. Les organes polliniques sont constitués de rachis aplatis avec ramification pennée subopposée, lesquels portent des synangiums terminaux. Le locule de chaque sac pollinique est tapissé d'une membrane tapétale lamellée et contient de nombreux grains de pollens et orbicules. Les grains sont petits, monosulqués et bisaccullés. L'ornamentation de l'exine de la paroi proximale est psilée, alors qu'en position distale la membrane de l'opercule est scabre. L'exine est composée d'une épaisse sexine se colorant faiblement et d'une exine fortement colorable. La sexine est latéralement tectée-alvéolée, devenant médialement presqu'homogène. Les alvéoles infra-tectales sont robustes et sont en continuité avec les unités endoréticulées des saccules. Les saccules sont eusacculés, montrant des endoréticulations attachées uniquement aux parois externes. Plusieurs grains immatures ont également été identifiés et indiquent que la nexine est entièrement lamellée et que les alvéoles infratectales ainsi que les lamelles de la nexine sont bien développées avant même que la synthèse du tectum soit complétée. L'auteur compare la dimension des saccules et l'ultrastructure du pollen des *Caytonanthus* avec celles des autres fougères à graines de la fin du paléozoïque et du mésozoïque produisant des pollens sacculés (Callistophytales, Glossopteridales, Corystospermales), et constate qu'elles sont plus petites et plus généralement remplies et munies d'endoréticulations plus épaisses. Il discute également l'état du caractère eusacculé chez les *Caytonanthus* en relation avec les implications phylogénétiques qu'on peut en tirer.

Mots clés : *Caytonanthus*, Caytoniales, mésozoïque, pollen, fougère à graines, ultrastructure.

[Traduit par la rédaction]

Introduction

The Caytoniales has received significant attention from both paleobotanists and neobotanists since the establishment of the order in 1925 as a new Jurassic group of angiospermous plants (Thomas 1925). The group is now known from rocks ranging in age from Late Triassic to Late Cretaceous from England (e.g., Thomas 1925; Harris 1964), Greenland (e.g., Harris 1932, 1937), Poland (Reymanówna 1973), Sweden (Lundblad 1948), Sardinia (Edwards 1929), Russia (Krassilov 1977), Japan (Kim and Kimura 1987), and North America (e.g., LaPasha and Miller 1985). No fossils of the group, however, have been recovered from Gondwana localities. The Caytoniales consists of three genera, including *Sagenopteris* (leaves), *Caytonia* (ovulate organs), and *Caytonanthus* (pollen organs). Dispersed pollen grains assigned to *Vitreisporites* have also been allied with the group. No specimens have been recognized showing organic attachment among the organs; consequently the three caytonialean taxa are taxonomically affiliated solely on the basis of field association and morphological similarity, especially regarding cuticular structure and the presence of *Caytonanthus* pollen grains in the micropyles of *Caytonia* ovules. In addition to *Sagenopteris*, *Caytonia*, and *Caytonanthus*, Harris (1964) also recognized the dispersed seed *Amphorispermum* as caytonialean but considered the putative caytonialean microsporophyll *Pramelreuthia* Kräusel (Kräusel 1949) as probably related to the Bennettitales.

It was originally suggested that the Caytoniales shared affinities with angiosperms based on the reticulate venation of *Sagenopteris* leaves, the carpel-like, closed morphology of *Caytonia* cupules, and the four-chambered pollen organs of *Caytonanthus* (Thomas 1925). Today, however, the group is widely considered to be distinctly gymnospermous based principally on the occurrence of *Caytonanthus* pollen in *Caytonia* micropyles (e.g., Harris 1940).

Caytonanthus is characterized by a pinnate morphology, with individual short pinnae arising from a main rachis in a subopposite to opposite pattern. The pinnae may fork a variable number of times and bear terminal synangia that are typically tetrasporangiate; however, pollen sac number may also vary. In situ pollen is relatively small, bisaccate, and has a single, distal sulcus. Several studies have figured and described *Caytonanthus* pollen grains as observed in transmitted light (e.g., Thomas 1925; Harris 1932, 1937, 1941, 1964; Van Konijnenburg-van Cittert 1971; Reymanówna 1973;

Krassilov 1977). Only three investigations, however, have examined in situ grains by electron microscopy (Krassilov 1977; Pedersen and Friis 1986; Zavada and Crepet 1986). Krassilov (1977) evaluated grains of *Caytonanthus tyrmensis* from the Tyrma locality, Siberia, Russia with scanning electron microscopy (SEM) and demonstrated that both the corpus and the sacci had smooth external surfaces and that the sacci were filled with "endosexinous ridges forming an irregular reticulum." Both SEM and transmission electron microscopy (TEM) were employed in the studies of pollen from *Caytonanthus arberi*, collected from the Cayton Bay locality, Yorkshire, England (Pedersen and Friis 1986; Zavada and Crepet 1986), and *Caytonanthus kockii*, obtained from Scoresby Sound, East Greenland (Pedersen and Friis 1986). The exine of *C. arberi* was described as tectate-alveolate and was often found associated with orbicules and tapetal membranes (Zavada and Crepet 1986). Pedersen and Friis (1986) showed that pollen grains of *C. arberi* and *C. kockii* were similar in both external morphology and exine fine structure. Although Pedersen and Friis (1986) did not illustrate exine ultrastructure in the cappa region, these authors were able to document faint nexine lamellae in some sections as well as the presence of well-defined endoreticulations within sacci.

In the present study, Middle Jurassic material of *C. arberi* from Cayton Bay was examined. In addition to clarifying a number of salient features regarding pollen ultrastructure, this paper documents information on pollen ontogeny and addresses several morphological characteristics of the synangium.

Material and methods

Fossil material and light microscopy

The Caytoniales is known from several Laurasian localities; however, two sites on the coast of Yorkshire, United Kingdom (Cayton Bay and Gristhorpe Bay), are the sources of the best preserved, most studied, and type material (e.g., Thomas 1925; Harris 1964). The fossil-bearing beds in Cayton and Gristhorpe bays are Middle Jurassic in age (e.g., Phillips 1875; Harris 1953) and have yielded *Sagenopteris*, *Caytonia*, and *Caytonanthus*, among an extremely diverse assemblage of plant remains (e.g., Seward 1900; Harris 1961, 1964, 1969, 1979; Harris and Miller 1974; Harris and Millington 1974).

Caytonanthus arberi microsporophylls with attached synangia and in situ pollen as well as dispersed synangia were isolated from shales collected at the Cayton Bay locality. Specimen Nos. J-3 86, J-3 91, J-3 96, and J-3 102 are well preserved and are housed in the Paleobotanical Collections of The Ohio State University.

The compressed organs were removed from the shales with a scalpel and dissecting probes. Synangia were demineralized in concentrated hydrochloric and hydrofluoric acids and thoroughly washed following each acid treatment. Several demineralized specimens were also cleared in concentrated nitric acid, while other synangia were mechanically macerated to isolate individual in situ pollen grains. For light microscopy, both individual palynomorphs and whole cleared synangia were mounted on slides and photographed using bright-field and differential interference contrast (Nomarski) illumination.

Electron microscopy

For SEM, synangia were attached to aluminum stubs with double-sided adhesive tape. Some synangia were teased apart using dissecting probes to expose their contents and the internal surfaces of pollen sac locules. Additionally, macerated pollen grains were pipetted directly onto polished aluminum stubs. All stubs were sputter coated with gold–palladium and examined using Hitachi S-500 and JEOL JSM-840 scanning electron microscopes at accelerating voltages of 15–20 kV.

For TEM, pollen grains were pipetted onto cellulose filters under suction, while whole synangia were gently placed onto filters. All 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), gradually infiltrated with Spurr epoxy resin, and embedded flat in shallow aluminum pans. Individual blocks overlaying particular pollen grains and synangia were then cut to obtain specific specimens and 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 stained with 1% potassium permanganate (5–30 min), 1% uranyl acetate (7–12 min), and lead citrate (0–20 min; Venable and Coggeshall 1965), and viewed on a Zeiss EM-10 transmission electron microscope at 60–80 kV.

Results

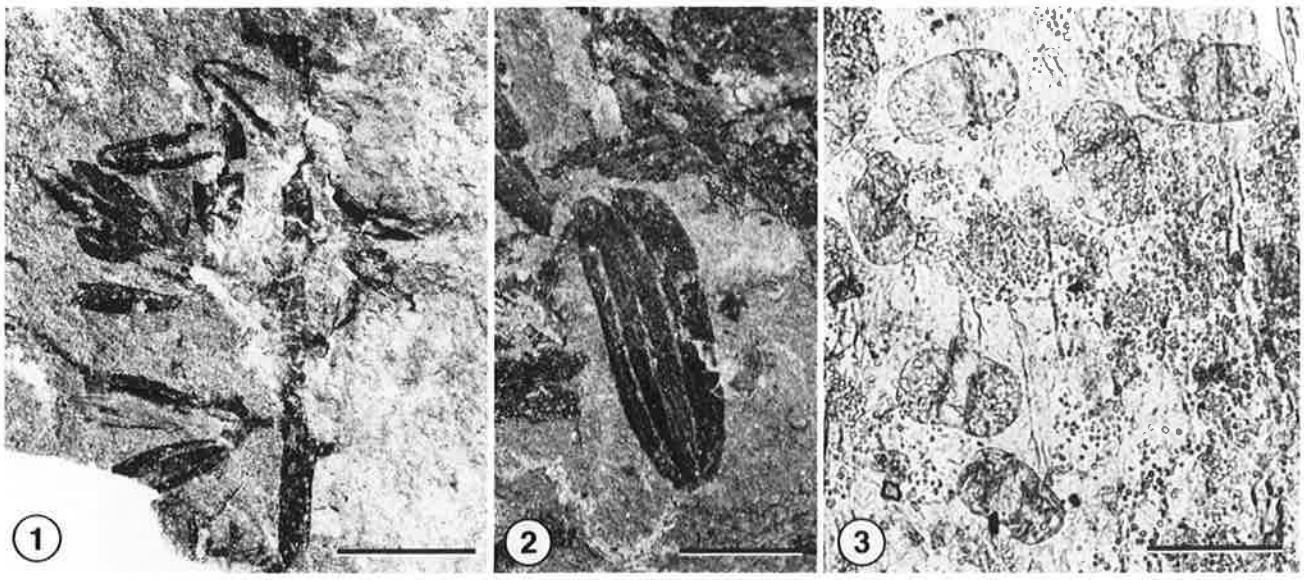
The *C. arberi* pollen organs studied here consist of narrow, flattened rachises, averaging 1.1 mm in width, which show subopposite branching. Branches are short, typically 1 mm in length, and may either bi-, tri-, or quadri-furcate to support the attachment of terminal, elongate synangia (Fig. 1). Entire organs are relatively small, averaging 15 mm in width (synangium to synangium) and 20 mm in length, although the specimens investigated are incomplete in length (Fig. 1). Synangia have rounded ends and measure approximately 5.1 mm in length and 1.8 mm in width (Figs. 1, 2). Individual pollen sacs are easily delimited at macroscopic levels by the presence of longitudinal furrows (Figs. 1, 2); specimens examined here typically have three to four pollen sacs.

Synangia are externally covered by a well-defined cuticle (Figs. 4, 5, 7, 9). The cuticle averages 1.32 μm in thickness and is in two parts; the inner region consists of a system of darkly stained fibrils or reticulations and is overlaid by a lightly stained amorphous region (Figs. 5, 7). This two-zoned organization is consistent in all synangia examined and is detectable in both uncleared and cleared specimens (Figs. 5, 7).

Individual pollen sac locules contain numerous in situ pollen grains, orbicules, and resistant tapetal membranes (Figs. 3, 4, 6, 8, 10, 11). Orbicules and tapetal membrane fragments occur throughout the synangia and are commonly found associated with pollen surfaces (Figs. 3, 4, 6, 8, 10, 11, 16, 17). Tapetal membranes are thin, averaging 0.05 μm in thickness, and commonly lamellated (Figs. 6, 8, 10, 11). Their fine structure is distinctly different from that of the pollen sac cuticles; tapetal membranes are thinner, lack reticulations, and stain more darkly (cf. Figs. 6, 8, 11 with Figs. 5, 7). The membranes may also be slightly irregular (i.e., finely scabrate); scabrae are similar in size and ultrastructure to the scabrae on orbicule surfaces (Fig. 8). Orbicules are spherical, with psilate to scabrate surface sculpture, and are somewhat variable in size, ranging from 0.32 to 1.33 μm in diameter. Orbicules are hollow, with a homogeneous wall averaging 0.40 μm in thickness (Figs. 6, 8, 10–12, 16, 17).

Pollen grains are relatively small, monosulcate, and bisaccate (Figs. 3, 12, 14). Sacci typically show lateral attachment (Figs. 12, 14), although in several grains the sacci are distally inclined. Grains average 23 μm in length (saccus to saccus) and 15 μm in width (Figs. 12, 14). In polar view, the corpus averages 11 μm in length and 15 μm in width (Fig. 12), while sacci range to 6 μm in length and 15 μm in width (Figs. 12, 14). Reliable corpus and saccus height measurements are not available for these grains because of their compressed nature.

The proximal wall of the corpus (cappa) is generally psilate; however, some grains have a finely ornamented surface (Figs. 12, 13). The distal wall is characterized by a broad sulcus, averaging 3.7 μm in width, that extends across the entire width



FIGS. 1–3. *Caytonanthus arberi*. Fig. 1. Morphology of pollen organ showing flattened rachis and branching pinnae with terminal, elongate synangia. Scale bar = 5 mm. Fig. 2. Dispersed synangium showing elongate morphology and longitudinally oriented grooves. Scale bar = 2 mm. Fig. 3. Detail of a cleared synangium showing in situ pollen grains and numerous spherical orbicules. Scale bar = 30 μm.

of each grain. By comparison, the apertural membrane is more scabrate (Figs. 14, 15). The exine is distinctly in two parts, composed of an inner, darkly staining nexine and an outer, lightly staining sexine (Figs. 18–24). Overall exine thickness averages 0.65 μm, while the sexine is typically more than three times thicker than the nexine, averaging 0.50 and 0.15 μm thick, respectively (Figs. 17–21).

When considering exine fine structure, it is important to note position and plane of section. When equatorial sections are examined from lateral (i.e., peripheral) grain positions, the sexine has an infrastructure composed of robust, platelike units (alveolae) averaging 0.20 μm in width and extending between a homogeneous tectum and the darkly staining nexine layer (Figs. 20, 21). A lightly staining, basal sexine component is for the most part absent; however, a very thin layer is detectable in some grains or sections (Figs. 23, 24). In more medial grain regions, the platelike alveolae are shorter, the tectum is thicker, and the overall sexine has a homogeneous ultrastructure (Fig. 19). The tectum averages 0.20 μm in thickness in lateral sections and is continuous with the outer saccus wall (Figs. 18–22). Sacci superficially appear to be completely filled with endoreticulations; however, discontinuity of the endoreticulum is evident in medial sections (Figs. 18, 19). Endoreticulations are also robust, having similar dimensions to the platelike, alveolar units located in lateral regions of the cappa (Figs. 18, 20–23).

The nexine is characterized by the presence of well-defined lamellae (Figs. 23, 24). In mature pollen grains (i.e., those with well-developed sacci and sporoderm layers), lamellae are generally only detectable in folded regions of the exine (Figs. 21–23). However, several immature grains have also been identified within synangia. These grains are commonly enveloped by orbicules (Fig. 16) and have a weakly developed tectum and infratectal alveolae (Fig. 24). However, the immature grains clearly exhibit lamellations throughout the entire nexine (Fig. 24). In both the mature and immature grains examined, the lamellae are similar in thickness, averaging 0.03 μm thick.

The apertural membrane consists of a very thin exine layer, with both sexine and nexine layers present. However, the lightly staining sexine component is patchy and present only in small amounts (Fig. 22), resulting in a scrabrate external surface of the sulcus (cf. Fig. 15). The thin sporoderm layer in the apertural region is the result of gradual, lateral thinning of both sexine and nexine layers (Figs. 19, 22).

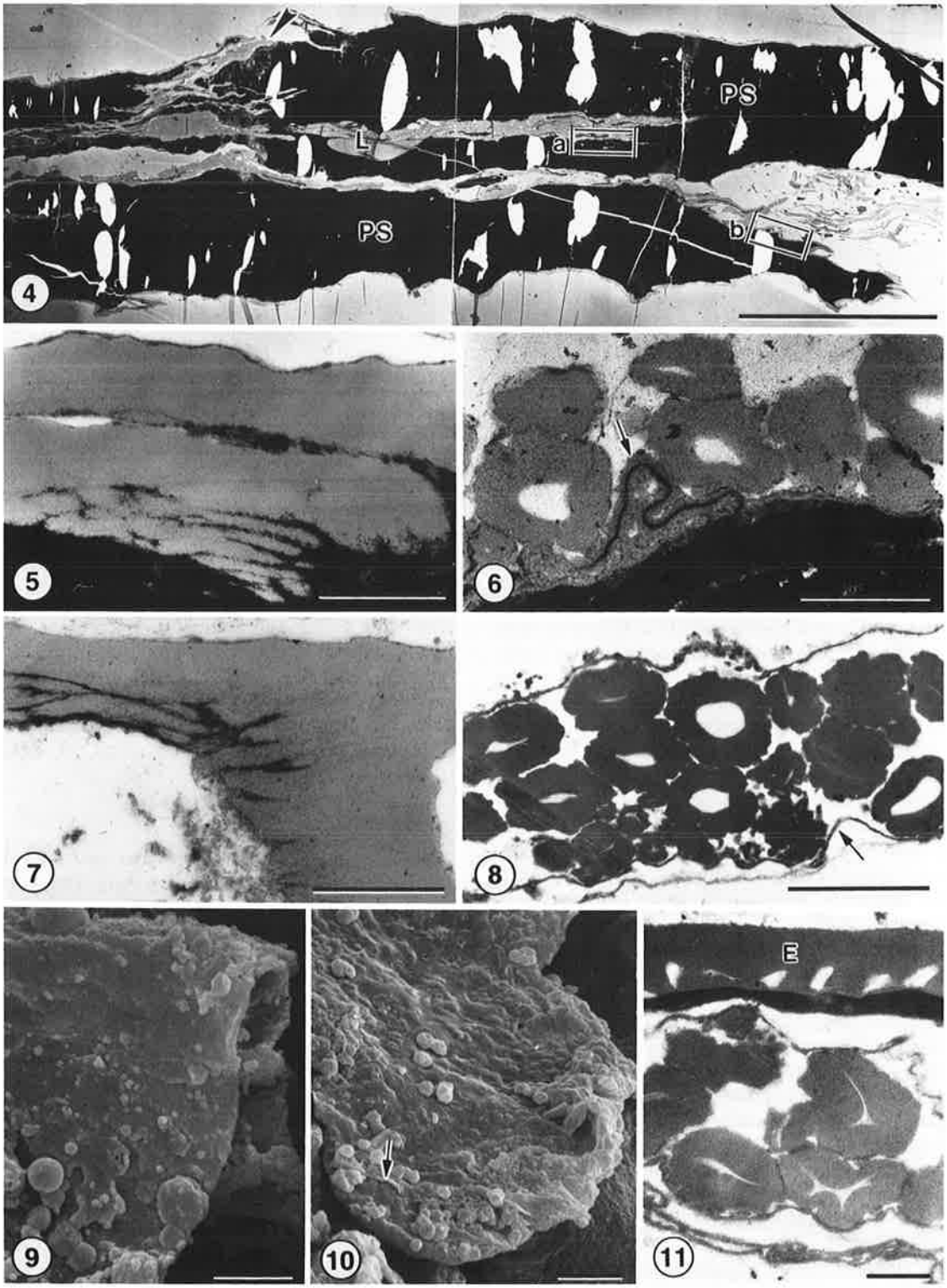
Discussion

Synangium cuticles

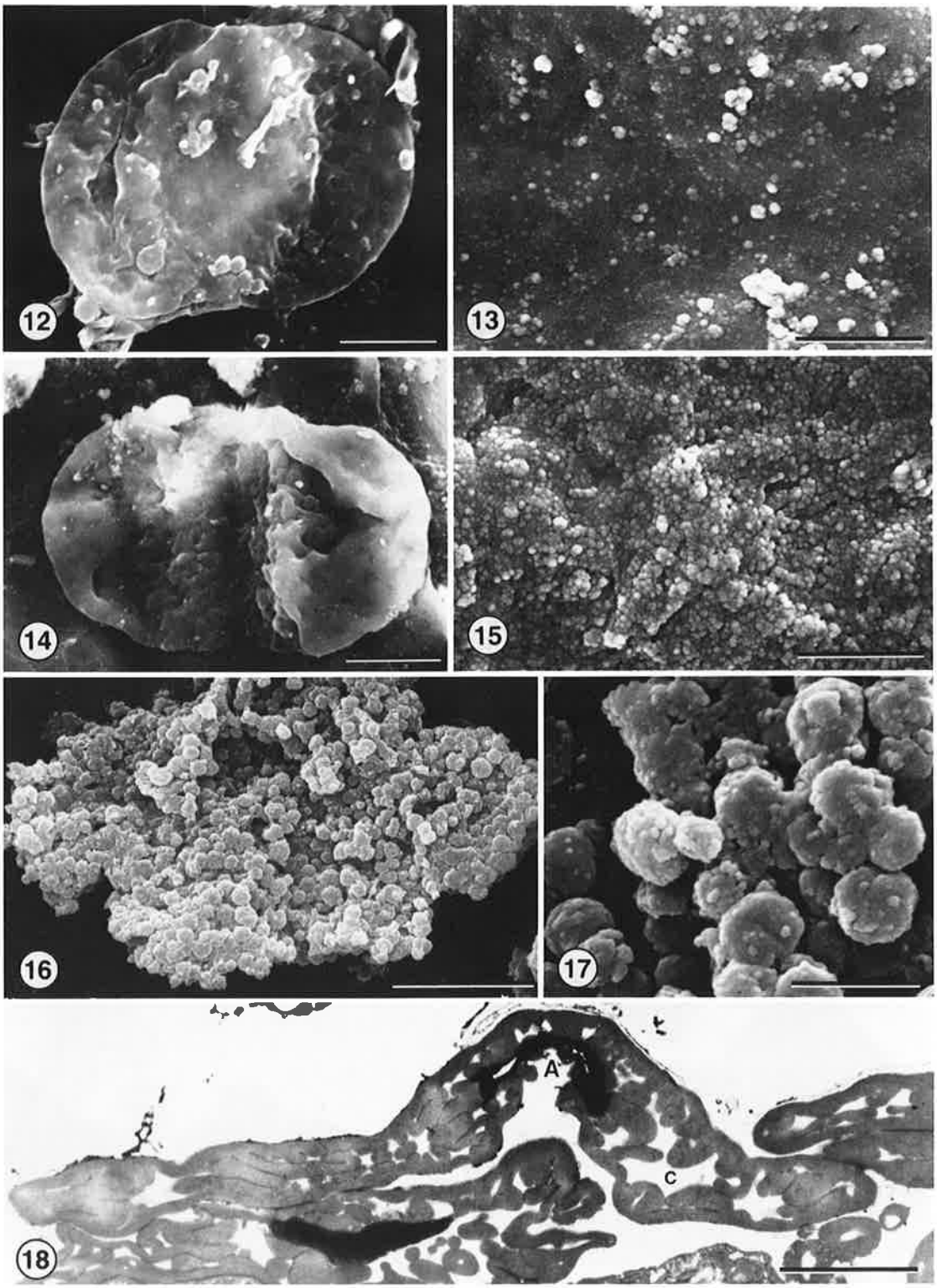
The present investigation provides new information on the fine structure of *Caytonanthus* synangia. Ultrastructural examinations confirm that the synangium cuticle is distinctly thinner than that of the microsporophyll rachis (J.M. Osborn, unpublished data) and indicate that the synangium epidermal cells (seen in transmitted light as fusiform and hexagonal in shape) are not well preserved but rather severely coalified. The cuticle is composed of a lightly stained, amorphous material with well-defined, darkly stained fibrillar units in its lower portion. This two-zoned organization (inner fibrillar layer and outer amorphous layer) is consistent throughout the entire cuticle and in all synangia sectioned. Fibrillae appear irregular in size and distribution and are basally attached to the underlying, darkly stained region of coalified tissues. It is possible that the fibrillae may represent folds and (or) cracks in the cuticle resulting from various compression-compaction phenomena that have become filled with the diagenetically altered cellular tissues. A more likely explanation, however, is that fibrillae are naturally occurring extensions of the formerly present, underlying epidermal cell walls similar to those observed in numerous extant plant cuticles (e.g., Holloway 1982).

Synangium contents: pollen, orbicules, and tapetal membranes

Several important features have been elucidated in the present study about pollen ultrastructure of *Caytonanthus*. The infratectal layer is not alveolate throughout the entire proximal wall, as was previously suggested (Zavada and Crepet 1986), but rather the infratectal alveolae gradually thin toward the median of the cappa resulting in a homogeneous structure in this region. In peripheral regions, infratectal alveolae of the



FIGS. 4–11. *Caytonanthus arberi*. Fig. 4. Transverse section through a portion of an uncleared synangium showing two darkly stained pollen sacs (PS). Only one locule (L) is visible in the upper pollen sac and is continuous with a possible dehiscence zone (arrowhead). The region of the pollen sac wall that lines the locule (box *a*) is illustrated in Fig. 6, while the synangium cuticle (box *b*) is shown in Fig. 5. Scale bar = 50 μm. Fig. 5. Detail of external synangium cuticle (similar to area shown in box *b* of Fig. 4). Note the darkly stained fibrillae extending into the lightly stained amorphous region. Scale bar = 1 μm. Fig. 6. Detail of pollen sac locule showing lamellated tapetal membrane (arrow) lining the locule (similar to area shown in box *a* of Fig. 4). Note also the associated hollow, spherical orbicules. Scale bar = 1 μm. Fig. 7. Detail of the external cuticle from a cleared synangium; note that the darkly stained fibrillae are still present (cf. Fig. 5). Scale bar = 1 μm. Fig. 8. Detail of the locule region from a cleared pollen sac showing numerous orbicules and tapetal membranes (arrow) that delimit the boundaries of the locule. Note also the fine scabrae on the surface of each orbicule. Scale bar = 2 μm. Fig. 9. Folded portion of a synangium cuticle showing several orbicules that have been liberated from a locule. Scale bar = 2 μm. Fig. 10. Single pollen grain within the locule of a cleared pollen sac; note that the grain is covered by thin tapetal membranes (arrow) and orbicules. Scale bar = 5 μm. Fig. 11. Ultrathin section through a grain similar to that illustrated in Fig. 10 showing the pollen exine (E) and associated tapetal membranes and orbicules. Scale bar = 0.5 μm.



FIGS. 12–18. *Caytonanthus arberi*. Fig. 12. Proximal view of a pollen grain showing psilate surface and several orbicules; note also the underlying endoreticulations in the right saccus. Scale bar = 5 μm. Fig. 13. Detail of cappa showing psilate ornament. Scale bar = 2 μm. Fig. 14. Distal view of a pollen grain showing broad sulcus extending the entire width of the grain. Scale bar = 5 μm. Fig. 15. Detail of apertural membrane showing scabrate morphology. Scale bar = 2 μm. Fig. 16. Distal view of a pollen grain completely covered with orbicules. Scale bar = 10 μm. Fig. 17. Detail of orbicules showing finely scabrate ornament. Scale bar = 2 μm. Fig. 18. Oblique section through a grain showing tectate-alveolate fine structure of the cappa, the distal aperture (A), and slightly distally inclined sacci. Note that although the sacci are extensively filled with endoreticulations, they do not span the entire saccus cavity (*c*) but are discrete in their attachment to the outer saccus wall. This is most prominent in the right saccus. Scale bar = 2.3 μm.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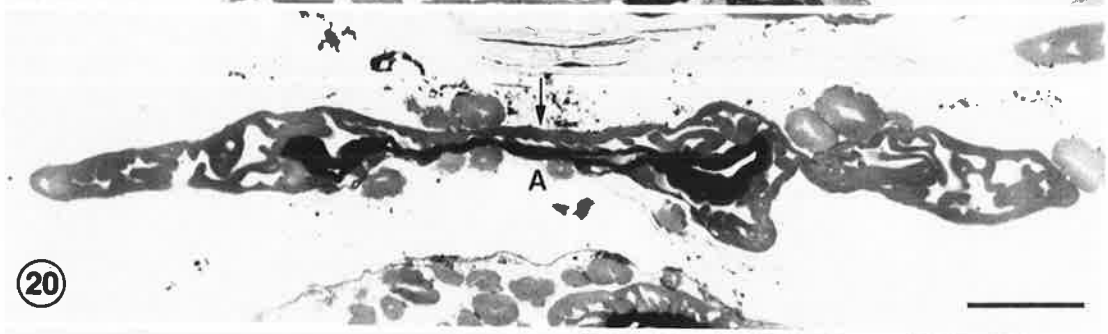
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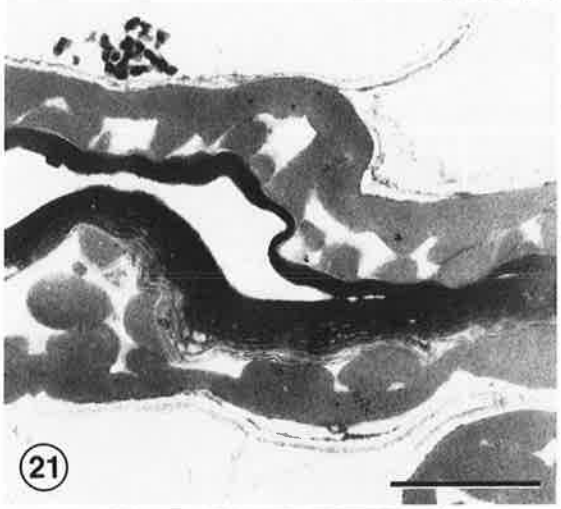
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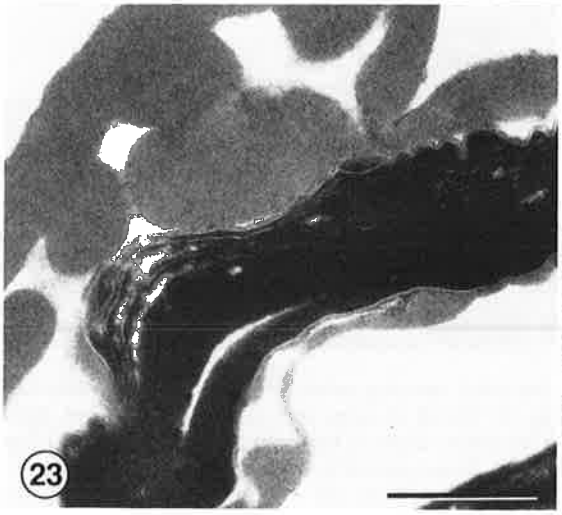
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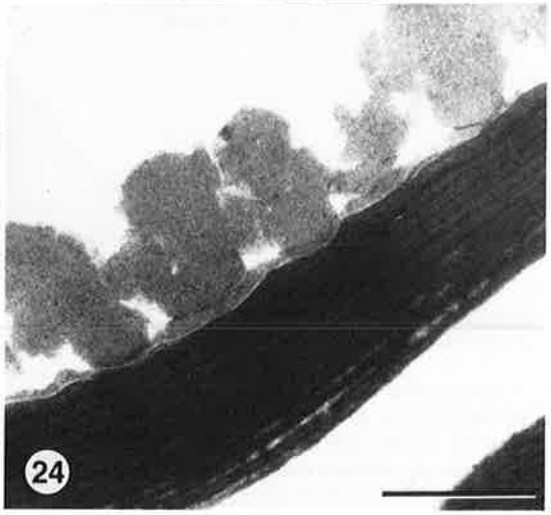
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cappa grade into the endoreticulations within the sacci. This type of organization, in which the proximal wall is medially homogeneous and laterally alveolate, with cappa alveolae grading into the endoreticular units of the sacci, is also present in the saccate pollen of another Mesozoic seed fern group, the Corystospermales (Osborn and Taylor 1993).

Another important character concerns the relative size of the infratectal alveolar units of the cappa and endoreticular units of the sacci. In the *Caytonanthus arberi* grains sectioned here, these units are strikingly more robust, especially in width, compared with those of the *C. arberi* grains sectioned by Zavada and Crepet (1986). However, they are similar in overall size to those of grains of both *C. arberi* and *C. kockii* investigated by Pedersen and Friis (1986). A related feature is the extent to which the platelike endoreticular units fill the sacci.

Pollen grains in which the endoreticulations extend continuously between the outer saccus wall and the saccus floor (i.e., lateral corpus wall) have been termed protosaccate, while those with endoreticulations restricted to the outer saccus wall and thus having an almost entirely hollow saccus cavity have been referred to as eusaccate (Scheuring 1974). Although the *C. arberi* grains examined here have an extensive network of endoreticulations within the sacci and superficially appear protosaccate, these units are indeed discrete in their attachment to only the outer saccus wall. Both medial sections and oblique sections that pass through medial regions of the sacci illustrate this morphological condition (Figs. 18–20). The sacci of the *Caytonanthus* grains sectioned by Pedersen and Friis (1986, p. 258) are reported as completely "infilled with exinal elements." This determination, however, appears to be based on interpretations of sections passing through grains in a polar plane that laterally glance the endoreticulum (Pedersen and Friis 1986, Figs. 5 (right saccus), 7, 8). In addition to such sectioning influences, the superficial appearance of a saccate pollen grain as protosaccate may be due to several other factors, including preservational phenomena, overall grain size, ontogenetic age, and reproductive biology (Osborn and Taylor 1994). The appearance of *Caytonanthus* grains as protosaccate is primarily the result of their compressed nature and their relatively small sacci.

Functionally, sacci are believed to play several critical roles, principally during pollination and pollination-related events. It is clear that sacci increase overall grain size without significantly increasing grain weight and thereby provide for efficient dispersal by wind (e.g., Crane 1986; Zavada 1991). Taking into account these functional considerations it is interesting to compare the relative sizes of sacci and endoreticulations of other Late Paleozoic and Mesozoic seed ferns that produced saccate pollen. To date, no information on pollen ultrastructure has been published for the Peltaspermales; however, the sacci of pollen grains of Callistophytales (Millay and Taylor 1974), Glossopteridales (Osborn 1991; Zavada 1991), and Corystospermales (Osborn and Taylor 1993 and references therein) are relatively large, especially in the latter, while the endoreticulations within these sacci are narrow. By comparison, the sacci of *Caytonanthus* grains are smaller and more extensively filled with thicker endoreticulations. Based on the relative size of the endoreticulations, it is possible that *Caytonanthus* grains were heavier than the pollen of other Mesozoic anemophilous seed ferns and not regulated as well harmomegathically.

The grains sectioned here also exhibit well-defined nexine lamellae and represent the most comprehensive documentation of these sporoderm lamellations in the group. Although Pedersen and Friis (1986, Fig. 10) described the nexine of *C. arberi* as lamellate, the individual lamellae are not particularly well preserved and do not appear to be distinct. In fact, in most of the mature grains sectioned here, lamellae are also either relatively faint or detectable only in folded regions of grains. However, discovery of a few grains preserved in early ontogenetic stages illustrates well-preserved lamellae throughout the entire nexine. The relative absence of distinct nexine lamellae in mature *Caytonanthus* grains is interpreted as a developmental phenomenon. In mature saccate pollen of extant conifers, discrete lamellae are also difficult to identify within the nexine. During pollen ontogeny of modern saccate conifers, nexine lamellae are easily detectable in immature grains but later become stretched and tightly appressed during saccus expansion in the free-spore phase (e.g., Kurmann 1990).

Historically, a few other aspects of pollen development in *Caytonanthus* have been addressed indirectly. Based on early examinations with transmitted light, Harris (1941) suggested that synangia may contain tapetal membranes. He wrote: "Besides the outer cuticle, most specimens provide vestiges of an inner obscurely cellular granular membrane to which the pollen grains often adhere; perhaps this membrane is the fatty matter of the tapetum hardened in preservation" (Harris 1941, p. 49). Zavada and Crepet (1986), however, were first to unequivocally demonstrate orbicules and resistant tapetal membranes at the ultrastructural level, although these authors did not recover any immature grains. Documentation of immature grains within synangia, along with the concurrent presence of orbicules and tapetal membranes, provides the opportunity to address several additional aspects of sporoderm development. Although intermediate ontogenetic stages have not yet been isolated from the material sectioned here, those immature grains examined indicate that the robust, infratectal alveolae and the nexine lamellae are well developed prior to complete synthesis of the tectum. Moreover, the surface scabrae observed on mature grains are similar in size and morphology to those on orbicule surfaces, as well as to the sporopolleninous units associated with tapetal membranes.

FIGS. 19–24. *Caytonanthus arberi*. Fig. 19. Medial, equatorial section through a pollen grain showing lightly stained sexine, darkly stained nexine, and distal aperture (A). Note the robust endoreticulations within the sacci that extend into the proximal corpus wall at the sites of attachment to the cappa; thus the cappa appears alveolate, except in the central region where it is nearly homogeneous (arrow). Scale bar = 2.4 μm. Fig. 20. More lateral section of the same grain illustrated in Fig. 19 showing change in fine structure of the cappa. The wall is no longer homogeneous centrally (arrow) but rather is alveolate throughout. Scale bar = 2.4 μm. Fig. 21. Oblique section through a grain showing the cappa (upper wall) with a well-defined tectum and infratectal alveolae, and underlying, darkly stained nexine. Note also the nexine lamellae in the folded region of the lower grain portion. Scale bar = 1 μm. Fig. 22. Oblique, transverse section through two distally inclined sacci showing nexine lamellae in the folded regions of the wall and thinning of both sexine and nexine layers over the apertural membrane (arrow). Scale bar = 1 μm. Fig. 23. Detail of left saccus in Fig. 22 showing lamellae in the folded nexine region. Scale bar = 0.5 μm. Fig. 24. Transverse section of an immature grain showing well-defined lamellae throughout the entire nexine and partially developed sexine; note the incomplete tectum as well as a thin, lightly staining basal layer. Scale bar = 0.5 μm.

An additional, noteworthy feature concerns the process of clearing specimens in nitric acid. Although clearing does not affect the gross ultrastructure of pollen grains, orbicules, or tapetal membranes, as determined by comparing cleared and uncleared specimens, it does affect the way in which these structures stain. In cleared specimens, grains, orbicules, and membranes apparently have a greater affinity for heavy metal stains, staining darker than those in uncleared pollen sacs.

Systematic implications

As noted above, in spite of Thomas' (1925) original suggestions of angiosperm affinities, the Caytoniales is widely regarded as gymnospermous and more distantly related to flowering plants. This view has been corroborated by several cladistic studies that link angiosperms as the sister group of Bennettitales, Pentoxylales, and Gnetales, collectively (anthophytes; e.g., Crane 1985; Doyle and Donoghue 1986). However, Doyle (1993) has suggested that angiosperms can be linked to either Caytoniales or Glossopteridales via several alternative, equally parsimonious cladograms. By comparison, Nixon et al. (1994) and Rothwell and Serbet (1994) have recently proposed that the Caytoniales and other higher seed ferns (Glossopteridales, Corystospermales, Peltaspermales) are not closely related to the anthophyte clade. These phylogenetic investigations have been based on a variety of morphological characters, including several palynological features.

Saccus composition (i.e., protosaccate versus eusaccate) is especially noteworthy, although it has been argued to have little value as a phylogenetic character (Osborn and Taylor 1994). Nixon et al. (1994) as well as Doyle et al. (1994) considered the Caytoniales to be protosaccate and have coded this character as apomorphic in their phylogenetic analyses. In another study, although not using saccus fine structure as a character per se, Doyle (1988) considered the Caytoniales as protosaccate and suggested that this condition is derived from the eusaccate form of the Callistophytales. It is clear now, however, that *Caytonanthus* pollen is in fact eusaccate. This new information necessitates reevaluation of how this character state is polarized in phylogenetic studies. Despite previous characterizations of *Caytonanthus* pollen and the apparent contrasting views of recent cladistic studies, it is clear that the Caytoniales remains a pivotal group in a phylogenetic context and underscores the importance of continued investigations of this group of Mesozoic seed plants.

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