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An ultrastructural and taxonomic study of *Valvisporites auritus* (Zerndt) Bhardwaj, a lycopsid megaspore from the middle Pennsylvanian of southern Illinois

ABSTRACT

An isolated megasporangium with *in situ* megaspores assigned to *Valvisporites auritus* (Zerndt) Bhardwaj has been collected from the Anna Shale Member, Carbondale Formation (middle Pennsylvanian), of southern Illinois. The specimen is preserved by authigenic cementation that allows the enclosed megaspores to remain uncompressed. The isolated megasporangium is assigned to *Lepidocystis* Lesquereux, emend. Wood, a genus established for disarticulated reproductive organs of lycopsid affinity. The specimen is most closely related to *Lepidocystis truncatus* Lesquereux (= *Polysporia mirabilis* Newberry), but is not assigned to this taxon, because 4 different reproductive strobili have been described in which megaspores assignable to *V. auritus* were produced. *Valvisporites* contains numerous species based upon differences in megaspore diameter, radial "ear" development and cingulum development. Examination of intact lycopsid fructifications demonstrates that when populations of megaspores are examined, characters used to separate species are invalid. The megaspore wall is composed of an anastomosing stratified pattern of sporopollenin rods similar to the structure reported for other extinct and extant heterosporous lycopods. It appears that lycopsid megaspores have retained a distinct organization throughout geologic time. Although there appear to be variants to the basic pattern, the primary organization of an ektexine composed of stratified anastomosing sporopollenin rods appears consistent. The ultrastructural organization of *V. auritus* adds additional evidence to the theory that lycopsid megaspores have remained basically unchanged in ektexine organization from the Carboniferous to the present.

INTRODUCTION

The Anna Shale Member, Carbondale Formation, Kewanee Group (Hopkins and Simon, 1975) at Carterville, Illinois has yielded a diverse, authigenically cemented megafloora (Gastaldo, 1975, 1977). Isolated lycopsid sporangia (SIPC [Southern Illinois Paleontological Collection] JJ1.28) assigned to *Lepidocystis* Lesquereux, emend. Wood, with *in situ* uncompressed megaspores, assigned to *Valvisporites auritus* (Zerndt) Bhardwaj, have been examined. The present study is concerned with the morphology, ultrastructure, and relationships of the megaspore.

Thirty-four megaspores, encrusted in a CaCO₃ precipitate, were exposed within a single megasporangium. A 5% hydrochloric acid solution was employed as the macerating agent to liberate the spores, which were prepared for light, scanning, and transmission electron microscopy. Some megaspores were prepared by staining with a solution of basic fuchsin and mounted in depression slides. Other megaspores were air dried, mounted upon Cambridge stubs and coated with two layers of 320Å gold. The specimens were examined at the SIU (Southern Illinois University-Carbondale) Center for Electron Microscopy on a Cambridge MK IIA (20 KV) SEM (scanning electron microscope). Ten megaspores were prepared for the TEM (transmission electron microscope) by staining with 5% potassium permanganate, dehydration, and embedding in Epon 812 (Millay and Taylor, 1974). Ultra thin sections ranging in thickness from 500 to 1000 μm, were cut on a Porter-Blum Sovall MTI ultramicrotome using glass knives. The sections were transferred to 200-mesh grids, post-stained in lead citrate, and examined on a Jeol TEM at the SIU School of Medicine, Springfield, Illinois.

Lepidocystis sp. and *Valvisporites auritus* (Zerndt) Bhardwaj

DESCRIPTION

Specimen JJ1.28 is an incomplete ironstone concretion consisting of part and partial counterpart, upon which are preserved the remnants of 3, possibly 4, isolated, dispersed megasporangia presumed to have been part of the same fructification (fig. 2). Two of the megasporangia exhibit only external morphological features; one appears to be partially preserved; the fourth sporangium is broken, revealing at least 40 uncompressed megaspores assignable to *Valvisporites auritus* (Zerndt) Bhardwaj (fig. 3). The megasporangia are oblong-elliptical in outline, 21–27 mm in length, 6–10 mm in width, and exhibit a longitudinal ridge extending almost the entire length of the sporangium. Maceration of the partial counterpart liberated 34 megaspores, as well as cuticular remnants of the megasporangium. The epidermal pattern manifested in the cuticular remains demonstrates a prismatic cellular arrangement,

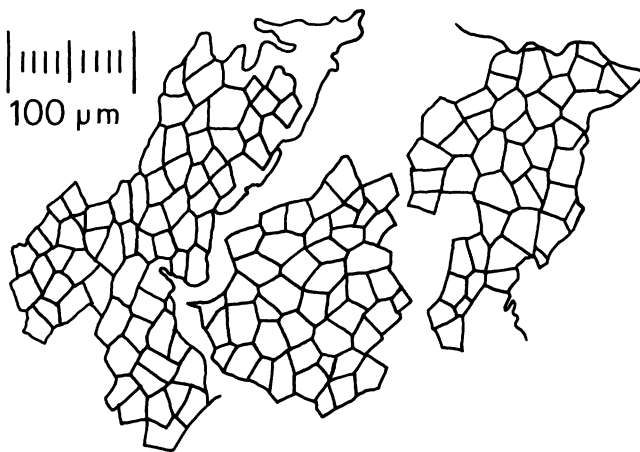


FIGURE 1
Camera lucida drawing of cuticular remnants liberated from *Lepidocystis* sp. (SIPC JJ1.28). Epidermal pattern demonstrates prismatic cellular arrangement, primarily composed of 5–6-sided cells, averaging 36 μm in length and 29 μm in width.

primarily composed of 5–6-sided cells, averaging 36 μm in length and 24 μm in width (fig. 1). There is no evidence of stomates on the outer surface of the megasporangium. The aspect of 5–6-sided prismatic cells appears to be consistent for those specimens of lycopod fructifications previously described (Coulter and Land, 1911; Arnold, 1930; Schopf, 1941; Abbott, 1963).

The sporangial contents are exclusively megaspores, assignable to *Valvisporites auritus* (Zerndt) Bhardwaj, based upon the following characters: outline triangular to trilobate with the development of bulbous projections at the radial extremities; diameter of the megaspores 771–1148 μm ; bulbous projections or “ears” less than one-half the body radius of the spore and less than the equatorial distance remaining between margins of the projections; triradiate ridges originating near the center of the proximal surface and standing in relief nearly 50 μm , extending to the base of the bulbous projections, whereupon their relief above the proximal surface is decreased (figs. 4, 5). The surface of the megaspore appears smooth when viewed by conventional light microscopy, with “papillae” contained on an “inner membrane” (Winslow, 1959), but manifests a different aspect when observed with the SEM. The proximal and distal polar surfaces of the megaspore are identical in structure and composed of an anastomosing network of sporopollenin rods averaging 0.45 μm in diameter (figs. 6, 7). This reticulate network extends across the entire distal surface, and across the curvaturae, or interray areas, of the proximal surface. Where the proximal and distal surfaces converge into the cingulum, the sporopollenin rods are densely aggregated (fig. 8). The cingulum, therefore, appears as a smooth equatorial rim encircling the megaspore. The bulbous projections, or “ears,” associated with the

radial extremities possess this reticulated pattern of sporopollenin when viewed proximally (fig. 9).

Transmission electron micrographs reveal a stratified pattern within the anastomosing exine (figs. 10–12). The exine is divided into a large ektexine ($\bar{x} = 65 \mu\text{m}$) and a thin and homogenous endexine ($\bar{x} = 650 \text{\AA}$). The ektexine widens toward the bulbous projections. The ektexine is composed of anastomosing sporopollenin rods which are further apart toward the surface of the spore wall. These sporopollenin units become compacted toward the endexine, and the stratification is evident. The ektexine is fused to the endexine, and the homogenous endexine appears lamellated (fig. 13).

EMENDED DIAGNOSIS

Valvisporites auritus (Zerndt) Bhardwaj (non Potonié and Kremp), **emend.**

Triletes auritus 1 ZERNDT, 1930, p. 46.

Triletes auritus var. *grandis*, typ. 11 ZERNDT, 1937, p. 584–585.

Triletes auritus var. *grandis* ZERNDT, 1940, p. 134.—DIJKSTRA, 1946, pl. 3, figs. 16, 17; pl. 4, fig. 23; 1955, p. 9.—PIÉRART, 1955, p. 592–593.

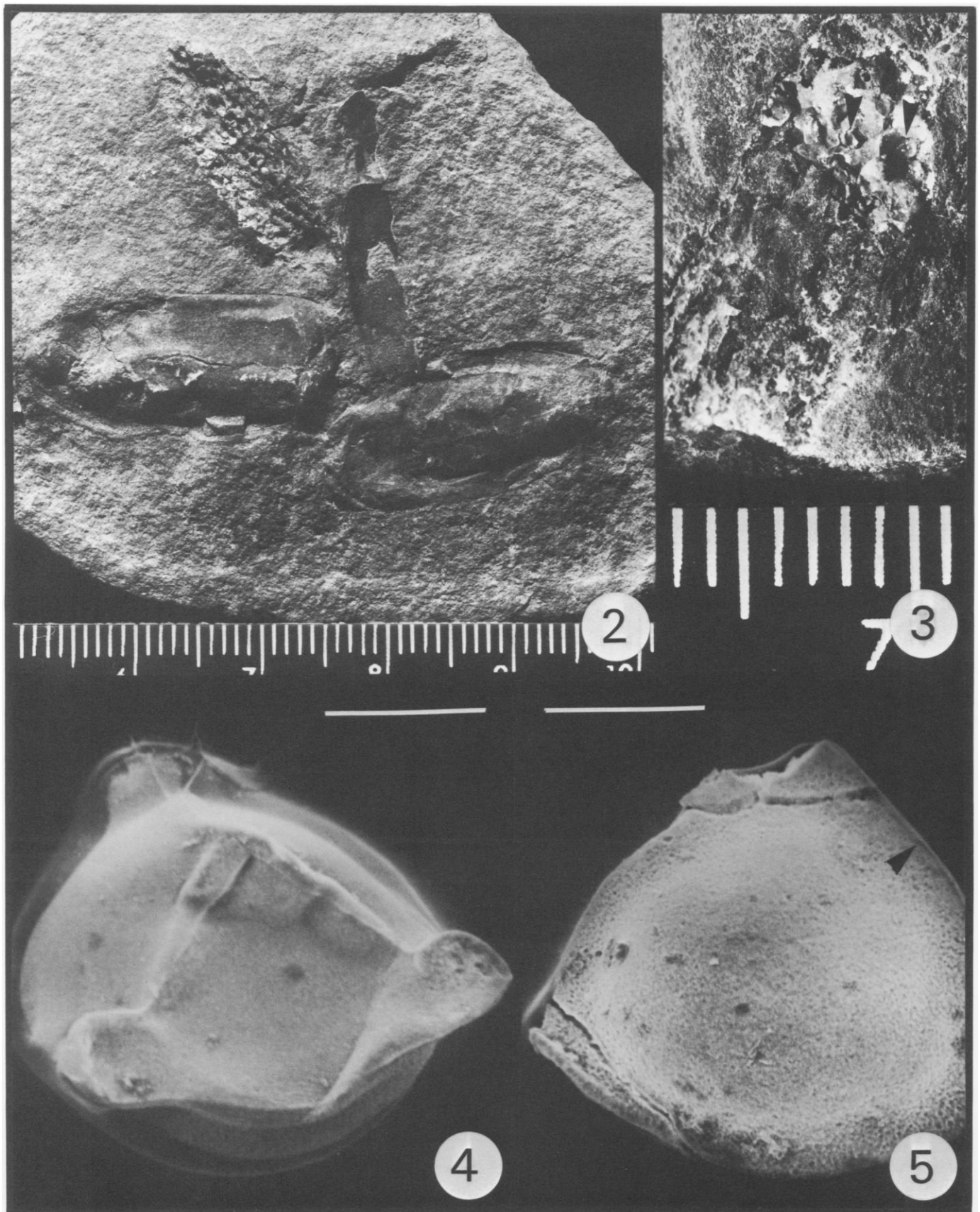
Valvisporites auritus (Zerndt).—POTONIÉ and KREMP, 1954, p. 134 (in part); 1955, pl. 6, figs. 38, 40, 41, 43 (in part).—CHALONER, 1958.

Valvisporites auritus (Zerndt).—BHARDWAJ, 1957, pp. 98–99.—KALIBOVA, 1958, p. 431.

Triletes auritus Zerndt (*sensu* Potonié and Kremp).—WINSLOW, 1959, p. 30.

Triletes auritus Zerndt.—ABBOTT, 1963, p. 106.

Megaspore triangular to trilobate in outline (compressed spores subtriangular to circular) viewed in distal and proximal polar view, with generally well-developed bulbous projections at the radial extremities, most evident in proximal polar view. Megaspores range in size from 520 to 1546 μm . In equatorial view, the proximal portion appears obtuse-triangular in outline, or pyramidal, with the development of “ears” at the radial extremities of the tri-radiate ridges, whereas the distal portion is somewhat semicircular in outline. The best developed appearance of these bulbous projections or “ears” are in proximal polar view, with the “ears” less than one-half the body radius in length and less than the equatorial distance remaining between “ear” margins in width; somewhat concave in the middle of the projection, and appearing decurrent upon the proximal margin near the juncture of the distal and proximal surfaces. The proximal and distal surfaces are structurally identical, composed of a network of reticulate sporopollenin rods averaging 0.45 μm in diameter and appearing smooth with “papillae” contained on an “inner membrane” when viewed with light microscopy. The reticulate network of sporopollenin units extends across the interray areas of the proximal surface, and over the entire distal portion up to the equatorial edge, or cingulum, where the sporo-



pollenin forms a smooth equatorial rim which encircles the megaspore. Triradiate ridges arise near the center of the proximal surface of the megaspore where they stand approximately 50 μm in relief and taper to the base of the bulbous projections, or "ear," whereupon there is a decrease in height above the surface. The exine is divided into a thick ektexine ($\bar{x} = 65 \mu\text{m}$) and a thin endexine ($\bar{x} = 650 \text{ \AA}$). The ektexine appears to be stratified throughout its vertical extent. The anastomosing sporopollenin rods are farther apart, near the outer surface of the ektexine, while toward the endexine, the sporopollenin rods become more compacted. The endexine is thin and homogenous, and appears slightly lamellated.

DISCUSSION

Taxonomy of *Valvisporites auritus* (Zerndt) Bhardwaj

Triletes auritus Zerndt, 1930 was established for megaspores which are triangular in outline and possess 3 small, bulbous projections at the extremities of the radiating trilete mark. Zerndt (1930) erected 16 different types of *T. auritus* and each form was numerically labeled. In addition to the numerical forms, Zerndt (1937) erected a variety, *grandis*, to encompass forms of *T. auritus* which were larger than those originally described. Because Zerndt referred such a large, and seemingly diverse, number of spores to *Triletes auritus*, subsequent workers deemed it necessary to define new species based upon the numerical types. Ibrahim (1933) erected a genus, *Valvisporites*, for triangular-shaped spores which possessed auriculae, or "ears" at the radial extremities, and Potonié and Kremp (1954) emended the genus to include all auriculate types of megaspores and microspores. *Valvisporites* Ibrahim, emend. Potonié and Kremp was classified in the section Auriculati, subsection Auriotrilletes, and a number of new species were erected to encompass the variability exhibited by *Triletes auritus* Zerndt.

Zerndt (1930) described *Triletes auritus* 1, and hence the holotype, from 2 obliquely flattened megaspores with small auriculae. The diagnostic characters established the size of the spores as 0.8–0.9 mm by measurement of the flattened spores. Potonié and Kremp (1955) removed *Triletes auritus* 1 from its taxonomic position

and placed it into *Valvisporites*, defining a range in size of 700–1100 μm for the megaspore. Bhardwaj (1957) remeasured the holotype material using the distance of the rays to the apex of the arcuate ridges, and concluded that the central body, alone, was 0.92 mm, while the total diameter of these megaspores, inclusive of the auriculae, was 1.1 mm. In addition, Bhardwaj (1957) noted that the arcuate ridges of the holotype material were as distinctly ledged as those in *Triletes auritus* var. *grandis*, and placed these 2 taxa into synonymy.

Bhardwaj (1957) believed that the material chosen to typify *Valvisporites auritus* (Zerndt) Potonié and Kremp was incorrect, and he removed those specimens described as *V. auritus* by Potonié and Kremp (1955) and established a new species, *V. westphalensis* Bhardwaj. Within this taxon he included a number of spores which had previously been assigned to *Triletes auritus* by various workers (Dijkstra, 1946; Kalibova, 1951; Piérart, 1955). *Valvisporites westphalensis* ranges in size from 0.5 to 1.0 mm, and was one of the smallest megaspores separated from the *T. auritus* complex. This taxon differed from the other small species, *V. augustae* (Loose) Potonié and Kremp and *V. nigrozonalis* (Stach and Zerndt) Potonié and Kremp, by possessing smaller ears and an apex prolonged into a vestibulum.

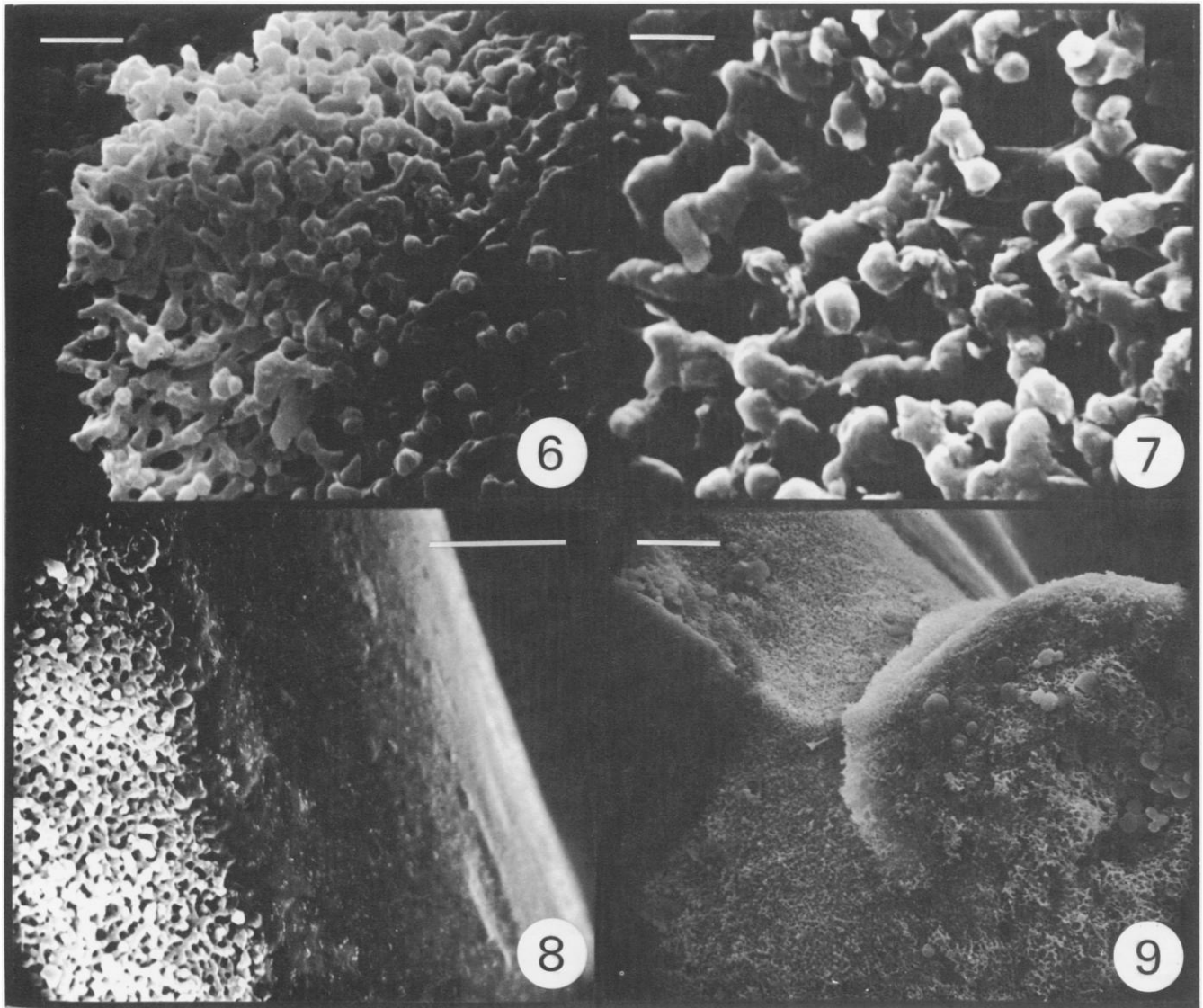
Bhardwaj (1957) redefined *Valvisporites auritus* (Zerndt) and based his holotype material upon the spores originally described by Zerndt (1930) as *Triletes auritus* 1. The taxon was described as possessing mostly large specimens, although smaller specimens were not unusual, with small auriculae as observed in polar view. Kalibova (1958) suggested an adjustment in size range of the spores from 0.6 to 1.6 mm in opposition to the measurements of Bhardwaj (0.8–1.2 mm) as well as a restriction in stratigraphic range to the Westphalian D and Stephanian. The stratigraphic ranges plotted by Kalibova (1958) for species erected from *Triletes auritus*, span Westphalian A to Stephanian strata. Bhardwaj (1957) differentiated *V. auritus* from *V. appendiculatus* (Maslankiewiczowa) Potonié and Kremp because the latter species possessed larger auriculae and hardly any cingulum, while *V. flavus* (Stach and Zerndt) Potonié and Kremp was described

FIGURES 2–5

2, *Lepidocystis* sp., SIPC JJ1.28a. Compression-impression of 4 authigenically cemented megasporangia, 2 preserved as external compressions, 1 incompletely preserved, the fourth exposed upon initial fracture. Within exposed megasporangium, numerous, uncompressed megaspores assignable to *Valvisporites auritus* (Zerndt) Bhardwaj. 3, JJ1.28b. Counterpart of fractured megasporangium with *in situ* megaspores assignable to *Valvisporites auritus* (Zerndt) Bhardwaj (arrows).

4, SEM of proximal polar surface of *Valvisporites auritus* (Zerndt) Bhardwaj. Megaspore triangular to trilobate in outline with development of bulbous projections at radial extremities. Bulbous projections, or "ears," less than one-half of body radius of megaspore. Although surface appears smooth viewed with light microscopy, surface has granular appearance under SEM. Scale 300 μm .

5, SEM of distal surface of *Valvisporites auritus* (Zerndt) Bhardwaj. Distal surface identical with proximal surface; at distal and proximal surface coverage (arrow) cingulum developed (see fig. 8). Scale 300 μm .



FIGURES 6–9

6, SEM of proximal surface of megaspore within curvaturae. Megaspore wall composed of anastomosing network of sporopollenin rods averaging $0.45\ \mu\text{m}$ in diameter. Reticulate network extends across distal and proximal surface, becoming dense and continuous at cingulum. Scale $2\ \mu\text{m}$.

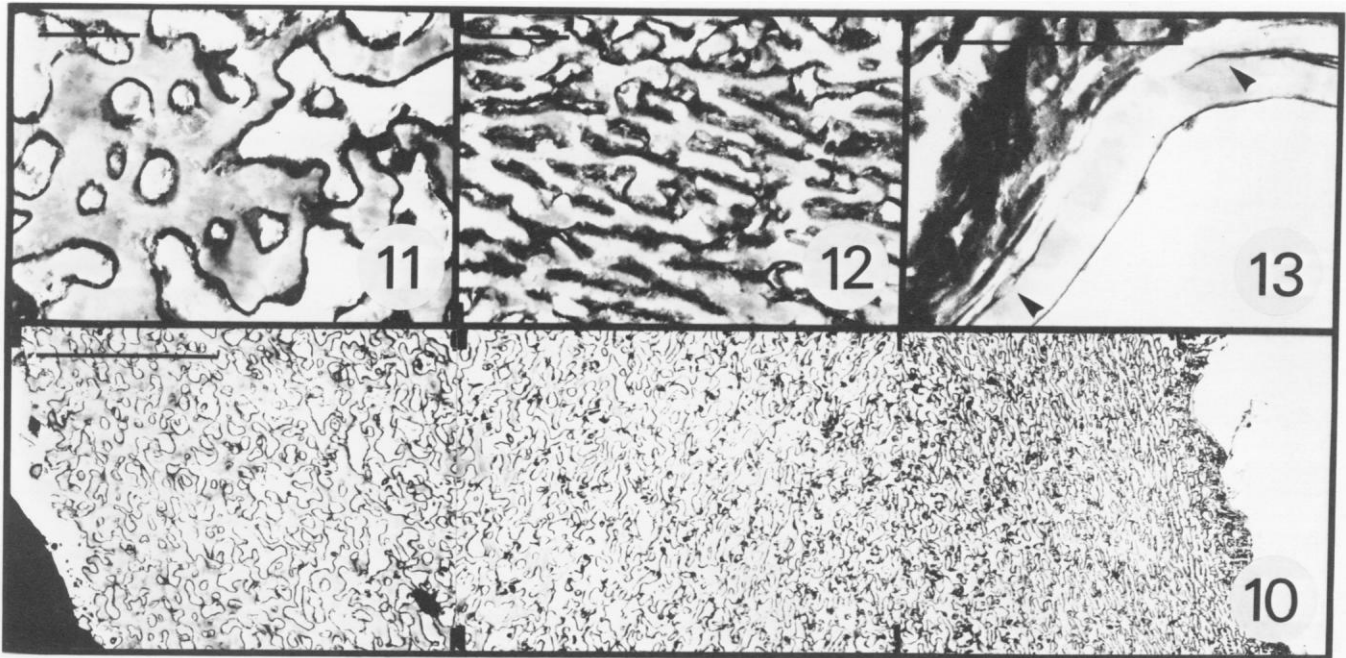
7, SEM of proximal surface of megaspore. Scale $1\ \mu\text{m}$.

8, SEM of equatorial cingulum (note position in fig. 5) as seen on distal surface. Surface pattern of distal face composed of three-dimensional network of anastomosing sporopollenin rods merging into cingulum of solid sporopollenin. Pitted markings on cingulum probably due to beam damage. Scale $10\ \mu\text{m}$.

9, SEM of proximal surface of megaspore, showing point of juncture with auriculae. Three-dimensional anastomosing network continuous from curvaturae to trilete mark and auriculae. Large spherical bodies preserved upon auriculae possibly ubish bodies. Scale $20\ \mu\text{m}$.

as differing in the prominence of rays which extend to the margin of the spore, as well as possessing smaller and pointed auriculae. Bhardwaj (1957) stated that a number of megaspores referred to *Triletes auritus* by Zerndt are referable to *Valvisporites nigrozonalis* (Stach and Zerndt) Potonié and Kremp. Dijkstra (1946) followed Zerndt's broad concept of the taxon and reduced *Valvisporites trilobus* Ibrahim, *Triletes nigrozonalis* Stach and Zerndt, and *Laevigatisporites sivanus* Ibrahim, as well as several other spores, into synonymy

with *Triletes auritus*. Bhardwaj (1957) properly concluded that the taxonomic status of *Triletes auritus* was "extremely confused." The subdivision of *Valvisporites auritus* into a number of species has been demonstrated not to reflect the true variation within the population of spores encountered within a parental organ. The delimitation of separate taxa based upon size, auriculae dimensions, and ray characteristics may be advantageous for stratigraphic palynology, but is unnatural when the megaspores are found *in situ*.



FIGURES 10–13

10, TEM of transverse section of megaspore wall. Megaspore wall exterior left of composite, interior at right. Large ectexine composed of anastomosing network of sporopollenin rods appearing stratified. Sporopollenin rods spaced farther apart at exterior of megaspore wall, more compacted toward interior. Thin, homogenous endexine apparently fused to base of ectexine. Section considered of average width, while width of megaspore wall greater toward auriculae. Scale 10 μm .

11, TEM of ectexine in distal position within megaspore wall. Sporopollenin rods fused and spaced farther apart than those of proximal region of the ectexine. Scale 1 μm .

12, TEM of ectexine in proximal position within megaspore wall. Sporopollenin rods more compacted than those of distal portion of ectexine. Scale 1 μm .

13, TEM of electron light endexine. Endexine fused to ectexine and seemingly lamellated (arrows). Scale 1 μm .

Lycopsid fructifications and their bearing on the taxonomy of *Valvisporites auritus*

Four strobili have been described in which megaspores assignable to *V. auritus* have been identified: *Lepidostrobos bartletii* Arnold, 1930, *Polysporia mirabilis* Newberry (Chaloner, 1958; DiMichele, Mahaffy and Phillips, 1979), *Lepidostrobopsis mansfeldii* (Lesqueux) Abbott, 1963 and *Lepidostrobopsis missouriense* (D. White) Abbott, 1963. Chaloner (1958) utilized the classification system of Potonié and Kremp (1955) and referred to the megaspores as *Valvisporites*, while Abbott (1963) retained the megaspores in *Triletes*. The classification system of Potonié and Kremp (1955) is followed in this study, even though the genus *Valvisporites* is artificial, and does not represent an assemblage of spores based upon parentage. The taxon was established as a convenience used to differentiate spores that possessed auriculae at their radial extremities.

Polysporia mirabilis Newberry, 1873 was a monotypic lycopsid "cone" taxon characterized by an axis surrounded by spirally arranged sporangia, which appeared to be attached directly to the axis. Chaloner (1953) provided some evidence to support the adaxial

position of the sporangia on the sporophyll, whereas DiMichele, Mahaffy and Phillips (1979) have described permineralized specimens and demonstrated that the shoots possess alternating fertile and vegetative zones. Therefore, *Polysporia* can no longer be considered a lycopsid strobilus. The close association of *Endosporites* microspores and *Valvisporites auritus* megaspores within the fertile areas suggests that microsporangia and megasporangia were borne in the same fertile zones (Chaloner, 1958; DiMichele, Mahaffy and Phillips, 1979). Chaloner (1958) synonymized a number of species of *Lepidocystis* with *Polysporia* on the basis of megasporangial and microsporangial contents. Although the specimen of *Lepidocystis* collected from the Anna Shale member may be *Polysporia*, it is not presently assigned to this taxon because other lycopsid fructifications are known to have possessed *V. auritus* megaspores. *Polysporia* is believed to be a herbaceous plant with an apparently upright habit.

The sporangia of *Polysporia* are reported to contain several hundred spores each. Chaloner (1958) demonstrated that the greatest diameter of flattened megaspores liberated from sporangia assigned to *Polysporia* ranged from 520 to 1360 μm (\bar{x} = 833 μm) for 173

spores, whereas megaspores liberated from *Polysporia* by DiMichele, Mahaffy and Phillips (1979) range from 725 to 1546 μm . An analogous situation obtains with the *Lepidocystis* sp. from the Carterville locality. Although only 34 megaspores were recovered from the counterpart, the range in size exhibited in this specimen alone was 771–1148 μm .

White (1899) described *Lepidophyllum missouriense* from the lower Coal Measures of Missouri. Abbott (1963) reevaluated the holotype and established a new genus, *Lepidostroboopsis*, which is primarily characterized as being megasporangiate with a pedicellate alation remaining horizontal, extending under the entire base of the sporangium, and at times overlapping the pedicel on either side. The unisexual strobilus possessed megaspores assignable to *V. auritus* and it is the character of the megaspore which separates this genus from other lycopsid strobilar taxa. In the same study Abbott (1963) designated a new combination, *Lepidostroboopsis mansfeldii* (Lesquereux) Abbott, basing her transfer upon sporangial shape, size and megaspores. The question as to taxonomic status of these 2 unisexual (megasporangiate) strobili will be treated in a future manuscript. These strobili are believed to be representative of arborescent lycopsids.

The report by Arnold (1930) of the megaspore *V. auritus* belonging to *Lepidostrobus bartlettii* Arnold should be treated with caution. *Lepidostrobus bartlettii* was described from the Pottsville series from a permineralized specimen in which the sporangia were dehisced and the spores liberated. The sporangia were reported to be remnants of wall fragments mixed with infiltrated matrix and only two megaspores, assigned to *T. auritus*, were found in the matrix. All other reports of North American *V. auritus* are from higher strata. From his identification of the megaspores, Arnold (1930) indicated that the cone was heterosporous. Due to the fact that only 2 megaspores were found in association with the fructification, and that no intact sporangia were found, the occurrence of *V. auritus* within this *Lepidostrobus* may be an artifact of transport. It is possible that upon reexamination of *L. bartlettii* Arnold, the specimen will demonstrate a relationship with *Polysporia mirabilis* Newberry.

The taxonomic status of *Valvisporites auritus* should reflect its natural range of characters as demonstrated by studies on parental organs. Dijkstra (1946) recognized one species of *Triletes auritus*, and lumped a number of species within this taxon. Other authors have used any number of characters to separate taxa. Potonié and Kremp (1956) distinguished *V. auritus* and *V. flavus* by a size demarcation of 1100 μm , but these species limits appear to be unwarranted because of the great range in megaspore size encountered

within parental organs. In addition, species delimitation was based upon dimensions of the auriculae and cingulum. DiMichele, Mahaffy and Phillips (1979) have demonstrated that megaspores from a population possess auriculae that may be well developed or indistinguishable. Since most taxa have been described from compressed megaspores, it is quite possible that the differences in auriculae dimensions are due to the state of preservation. It can be noted that the best exposure of the auriculae is in the proximal view, and when compressed, observation from the polar view (distal or proximal) may provide varying degrees of exposure. This condition has apparently given rise to numerous artificial species based upon "ear" characters. The degree of cingulum development had been used to differentiate species at the light microscope level. Again, this character may be dependent upon maturation of the megaspore, and vary considerably within the population of megaspores. Taylor and Eggert (1969) noted that the differences in structures exhibited in specimens of *Lycospora* may be due to differing depositional environments, or may represent different stages of spore development. It is possible that a number of species of *Valvisporites* which have been based upon forms of *T. auritus* are just population and age variants and should be treated under a single taxon. The concept of *Valvisporites auritus* should remain rather broad in definition due to the wide range of size known to occur within the natural population. There is no attempt made herein to revise the megaspores of the genus *Valvisporites*, although a definite need is recognized.

Ultrastructural studies of lycopsid megaspores

The use of electron microscopy in the study of Paleozoic pollen and spores has added new insights into structural and ultrastructural relationships. Taylor and Eggert (1969) reported on the structure of Carboniferous lycopsid spores assigned to *Lycospora* Schopf, Wilson and Bentall utilizing only SEM, and Zimmerman and Taylor (1970) described the ultrastructural components of several megaspore membranes including *Mazocarpon oedipternum* Schopf. Kempf (1971a, 1971b) studied lycopsid megaspores from Mesozoic deposits of Germany and Denmark using TEM, and differentiated perine and exine layers. Brack and Taylor (1972) and Taylor (1973) studied the ultrastructural organization of *Endosporites*, while Taylor (1974) and Taylor and Brack-Hanes (1976) described the ultrastructure of a *Cystosporites*, a large functional megaspore found in some species of *Lepidocarpon* and *Achlamydocarpon*.

Valvisporites auritus has revealed a number of characteristics through electron microscopy which are undetectable with conventional light microscopy. These ap-

pear to be correlative with those of other lycopsid megaspores. The anastomosing sporopollenin rods composing the ektexine are imperceptible at the light microscope level. The surface of the megaspore has been described as smooth, but scanning electron micrographs reveal that both the polar proximal and distal surfaces, as well as the auriculae, are structured by the sporopollenin rods. A smooth cingulum, not generally noticeable with light microscopy, encompasses the equatorial region of the megaspore, and is composed of an aggregation of sporopollenin rods. The presence of a cingulum is reported to occur in megaspores of *Isoetes* and some species of *Selaginella* (Henbest, 1935; Berthet and Lecocq, 1977), and appears to have been retained in some lycopsid megaspores. The ektexine of *V. auritus* appears to be stratified with the sporopollenin units spaced farthest apart at the distal portion of the ektexine, and closer together at the proximal portion of the megaspore wall.

The apparent stratification of sporopollenin units in the ektexine appears to be a consistent feature within the heterosporous extinct and extant Selaginellales and Isoetales and other heterosporous forms. Zimmerman and Taylor (1970) described the ultrastructural organization of *Mazocarpon oedipternum* Schopf. Although no complete section of the megaspore was examined due to the extreme thickness of the membrane, a number of features were reported. The surface of the spore, referred to as the "tectum," was covered with intrasporangial parenchymatous tissue referred to as "ramentum" by Schopf (1941). A clearly defined exine was described as composed of a fine spongy layer ranging from 12–50 μm in thickness. A thin nexine (=endexine?) was found to be internal to a complex anastomosing network of baculae termed the sexine (=ektexine). The baculae (sporopollenin units) were observed to be closely packed in the inner region and more widely spaced near the tectum. Zimmerman and Taylor (1970) noted that this organization appears very similar to that described for *Selaginella pulcherrima* (Pettit, 1966).

Taylor (1974) described the ultrastructural organization of viable and abortive megaspores of 2 lycopsid genera, *Lepidocarpon takhtajanii* Snigirevskaya and *Achlamydocarpon belgicum* Lambry. It appears that the organization of the megaspore wall of *L. takhtajanii* differs drastically from that observed in *V. auritus*, while the megaspore of *A. belgicum* appears similar. *Lepidocarpon takhtajanii* possesses a single, functional megaspore with 3 abortive megaspores within the megasporangium. The outer portion of the megaspore is constructed of delicate, elongate fiber-like units that branch and anastomose to form a superimposed interlacing of platelike layers. This arrangement of sporopollenin units is very different from *V. auritus* where the

megaspore wall is composed of a three-dimensional reticulate network of anastomosing sporopollenin rods. The ultrastructural organization of *A. belgicum* is similar to that described for *V. auritus*, in that the megaspore wall is composed of an inner homogenous layer that supports a thicker anastomosing zone of small, irregularly shaped sporopollenin rods, closely compacted.

Another species of *Achlamydocarpon*, *A. varius* (Baxter) Taylor and Brack-Hanes, 1976 was described, in which the large functional megaspore was examined at the ultrastructural level. The megaspore differs from *Valvisporites auritus* in size and the aggregation of sporopollenin into a massa. Taylor and Brack-Hanes (1976) believed that the spherical units, which have been observed to be continuous with the membranaceous remnants on the spore exine, represent remnants of the functional tapetal system in the form of orbicules ("ubish bodies") and associated tapetal membrane. The sporoderm is divided into 3 distinct zones consisting of (1) a series of muri (=sporopollenin rods) and interconnected lamina, (2) a large, irregularly shaped electron dense unit of sporopollenin possessing the same morphological characteristics as the massa region, and (3) a uniformly thick layer that is believed to represent nexine. Megaspores extracted from *Achlamydocarpon* are assignable to the dispersed spore genus *Cystosporites*, and Taylor (1974) indicated that the wall of this megaspore is typically homogenous with the total thickness of the wall constructed of a series of reticulate muri, or sporopollenin rods. The specimen described by Taylor (1974) differs from the specimen described by Taylor and Brack-Hanes (1976) in exine differentiation, and it is suggested that in *A. varius*, the large sporopollenin units of the middle layer may constitute accretation materials which were not differentiated into the anastomosing network characteristic of the remainder of the exine. Weatherby (1944) remarked that the appearance of sculpturing of *Selaginella* microspores and megaspores varies with age, but it is consistent within mature members of a species. It is possible that the globular subunits comprising the middle layer of the exine may either be due to a maturation phenomenon, or it is a true characteristic of a separate taxon.

The basic organization of a reticulated, anastomosing network of sporopollenin units appears to be present, to some degree, within the majority of Carboniferous lycopsid megaspores, studied ultrastructurally. This framework also appears to be retained by megaspores of lycopsid affinity in Mesozoic sediments. Kempf (1971a) described the ultrastructure of a lycopsid megaspore, *Horstisporites reticulatus* from Triassic strata of Germany. The perine (=ektexine?) was

described as showing a monozonal formation consisting of sporopollenin threads, coalescing centrifugally, forming a three-dimensional network. The exine (=endexine?) is described as being thin and lamellated, homogeneous in nature and underlying the perine. The ratio of perine to exine is reported to be 50:1 (Kempf, 1971b). This type of monozonal formation resembles some species of the extant *Selaginella* (i.e. *S. selaginelloides*).

Kempf (1971b) described 5 additional megaspore taxa of lycopsid affinities from the Mesozoic strata of Denmark. *Banksisporites pinguis* (Harris) Dettman was described as possessing a perine composed of anastomosing sporopollenin threads and a perine: exine ratio of 15:1. *Horstisporites kendallii* Kempf and *Nathorstispori hopliticus* Jung were reported to have a perine: exine ratio of 20:1. Both taxa exhibit a perine structure which appears divided into an inner zone composed of sporopollenin threads oriented concentrically, and an outer zone of threads giving rise to an irregular and dense network. *Margaritatisporites turbanaeformis* (Harris) Kempf was described as possessing a three-layered, concentrically arranged, perine. The perine: exine ratio approaches 35:1. *Istisporites murrayi* (Harris) Kempf is reported to have a thick perine in which the space between sporopollenin units is reduced to the extent to which the structure appears almost solid.

Kempf (1971b) proposed that through time the functional importance of the exine, as defined by him (=endexine?), has increased, while contemporaneously, there has been a reduction in the perine (=ektexine?). This supposition is based upon ultrastructural analyses of Carboniferous megaspores, such as *Setosisporites hirsutus* (Kempf, 1971b) which appears to possess a perine: exine ratio approaching 250:1. Examination of lycopsid megaspores in Mesozoic sediments reveals a decrease in the ratio, while extant species of *Selaginella* apparently possess the smallest such ratio. Many more ultrastructural studies of lycopsid megaspores are needed before a complete evaluation of Kempf's ideas can be made.

Atzelius, Erdtman and Sjöstrand (1954) studied the ultrastructural organization of *Selaginella selaginoides* megaspores and observed a three-dimensional network of rounded sporopollenin bars in the outer part of the exine. Martens (1960) found that *Selaginella myosorus* (Souv.) Alston had a specific orientation of the sporopollenin units within the ektexine, while Stainier (1965) observed in *S. myosorus* and *S. kraussiana* an almost identical structure of the exine to that of *S. selaginoides*. Pettit (1966) observed concentric zones of ektexine in *Selaginella pulcherrima* megaspores with each zone differing in the amount of interstitial space between

sporopollenin units, whereas Tryon and Luagandon (1978) examined megaspores of *S. martensii* and *S. galeottii* and reported an anastomosing pattern and increasing compaction in zones D, C, and B.

SUMMARY

It seems evident that the ultrastructural framework of megaspores of lycopsid affinities have retained a distinct organization throughout geologic time. Although there appear to be variants to the basic pattern of organization, such as *Istisporites murrayi* (Kempf, 1971b) and megaspores liberated from *Achlamydocarpon varius* (Taylor and Brack-Hanes, 1976), the primary organization of an ektexine composed of stratified anastomosing sporopollenin rods appears consistent. The ultrastructural organization of *Valvisporites auritus* (Zerndt) Bhardwaj adds additional evidence to the theory that lycopsid megaspores have remained basically unchanged in ektexine ultrastructural organization from the Carboniferous to the present.

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