Two New Plant Genera of Pennsylvanian Age from Kansas Coal Balls

By SERGIUS H. MAMAY

A SHORTER CONTRIBUTION TO GENERAL GEOLOGY

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Descriptions and illustrations of
Tyliosperma *and* Sclerocelyphus
fructifications

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By Sergius H. Mamay

ABSTRACT

The strip-mined coal producing area of southeastern Kansas has recently been discovered to contain coal balls in great abundance. The fossil plant contents of these coal balls are extremely diverse; as a result of the present investigation of this material, two new genera of fructifications may now be added to American Pennsylvanian floral assemblages. The generic names *Sclerocelyphus* and *Tyliosperma* are proposed for these fructifications. *Sclerocelyphus* is a peculiar sporangium containing numerous small spores; in certain features it resembles the megasporangium *Mittagia seminiformis* Lignier. *Tyliosperma* is a small cupulate pteridospermous seed whose structural simplicity suggests a primitive position among the seed ferns.

INTRODUCTION

This paper deals with two new Pennsylvanian fructifications that were found in coal balls collected at the strip pits of the Pittsburgh and Midway Coal Company near West Mineral, in southeastern Kansas. Investigations of coal balls from this recently discovered rich locality are now being conducted in several American paleobotanical laboratories. Baxter (1951) recently published a report of this coal ball occurrence; Delevoryas and Morgan (1952) have described a new species of *Tubicaulis* (*T. multiscalariformis*) from this locality, and a preliminary survey of the flora has recently appeared (Andrews and Mamay, 1952). Although these studies are yet in their incipient stages, it has already become obvious that the vegetable content of these petrifactions represents probably the most diverse floral assemblage yet discovered in coal balls. Thus, distinct new entities, such as that described by Delevoryas and Morgan and those to be described in this paper, may reasonably be expected to be found in some abundance as the investigations progress.

The two fructifications that form the subject of this paper entail several fundamental points of morphological interest, which will be discussed at some length in the conclusion. Aside from this, further interest lies in their appearance as two new generic additions to American coal-ball floral assemblages.

Sclerocelyphus, the first fructification to be discussed, is a peculiar sporangium containing numerous small spores; thus, it may be either the microsporangium of a heterosporous plant or the fructification of an otherwise unknown homosporous form. Although there is some evidence at hand in favor of it being a *microsporangium*, this cannot be definitely established at present. *Sclerocelyphus* is, in several considerations, a most enigmatic fructification. It differs strikingly from any fructification hitherto recorded in American fossil floras; indeed, the single fossil plant with which it compares favorably as to structural details is the megasporangium described by Lignier (1913) as *Mittagia seminiformis*, found in coal balls from the Koksflöz in Lower Silesia.

Tyliosperma, the second fructification, is a small, simple seed whose organization indicates affinities with the pteridosperms. While its gross morphological features are reminiscent of such other Paleozoic seeds as *Conostoma* and *Lagenostoma*, its structural details are on the whole simpler and convey the impression of a more primitive fructification. Aside from its structural simplicity, *Tyliosperma* is of additional interest in that its organic connection with a cupulate organ has been observed. Such instances of demonstrable attachment between petrified seeds and supporting organs are rare; the classical investigation of *Lagenostoma lomaxi* by Oliver and Scott (1904) may be cited here as the outstanding example of this sort of discovery. Unfortunately, however, the single specimen of *Tyliosperma* in which this connection has been demonstrated does not shed any light upon the question of the identity of the stem that bore these interesting seeds or the position they occupied on the parent plant.

SOURCE, AGE OF THE MATERIAL

The specimens were found in coal balls collected at the strip pits of the Pittsburgh and Midway Coal Company, about 4 miles south of West Mineral, Kans. (Columbus Quadrangle, Cherokee County). The Fleming coal, in which these petrifications occur, lies in the upper part of the Cherokee shale, which belongs to the Desmoinesian series of the Pennsylvanian as classified by the Kansas State Geological Survey (see Abernathy, 1946). The collection was made in March 1950 with Dr. H. N. Andrews, of Washington University, St. Louis, Mo., who kindly deposited the specimens with me for investigation.

To the best of my knowledge, both *Sclerocelyphus* and *Tyliosperma* are unique to coal balls from this locality.

SYSTEMATIC DESCRIPTIONS

Sclerocelyphus oviformus Mamay, n. gen., n. sp.

Plate 21, figures 1–12

General description.—A single coal ball (WCB 711–B) provided all the *Sclerocelyphus* material on hand. A preliminary saw cut exposed a group of several intimately associated sporangia; these were investigated by means of a closely spaced series of 110 Parlodion peel sections.

During the preparation of the peel series, about 60 essentially complete sporangia were exposed. These all lie fairly close to each other (within an area of not more than about 2 cm in diameter in any single section), and many are appressed to each other with a consequential flattening of contiguous sporangial wall surfaces. This feature is shown in plate 21, figure 12.

The orientation of the group of sporangia shown in plate 21, figure 10 is of particular interest. These sporangia all lie with their axes oriented in nearly the same direction; this suggests that they were preserved in essentially natural positions without first having become detached from the supporting appendages of the plant that bore them. Had they been shed prior to fossilization, there is little likelihood that they would have fallen into as uniformly oriented a group as this.

Isolated sporangia that were not subjected to pressure with others display an essentially spherical shape. The largest ones attain diameters of 2 mm. Aside from their relatively large proportions, the sporangia are characterized by the following combination of features:

1. A complex sporangial wall, consisting of two distinct tissue layers: an outer layer (a single cell thick) of prismatic palisade cells with heavily thickened walls (the palisade cells are dark brown, and to the naked eye they readily serve to distinguish the sporangia from the surrounding matrix); and an inner tissue, consisting of several layers of thin-walled parenchymatous cells.
2. A "cushion" or somewhat cupshaped aggregate of sclerified cells in the base of the sporangium.
3. Slender vascularized pedicels, the xylem of which enters into the bases of the sclerotic cushions.
4. Spore masses consisting of hundreds of small, spherical spores with trilete markings and highly distinctive ornamentation.

The sporangial wall.—The sclerotic outer layer of the sporangial wall shows some variation in thickness (pl. 21, fig. 12). In places where it is appressed to that of an adjacent sporangium, it may not exceed 40μ in thickness; otherwise, it reaches a thickness of 100μ. As suggested by Hoskins and Cross (1943, p. 127) in reference to the sporangia of *Bowmanites trisporangiatus*, this variation in thickness may well be a growth phenomenon, the less thickly developed portions of the wall being a reflection of pressure produced during the early stages of development of a compact group of sporangia. A similar variation in wall thickness is present in sporangia of *Mittagia seminiformis* (see Lignier, 1913, p. 54); Lignier also suggested ontogenetic appression, writing:

> * * * leur juxtaposition est en réalité *la conséquence d'une croissance côte à côte sur un même organe* c'est-à-dire, en somme, *qu'ils appartenaient à un même sore.*

In one instance the appression of two sporangia was apparently great enough to produce a slight interlocking of their outer wall cells during ontogeny. This, however, is not sufficiently consistent of occurrence to provide grounds for a synangial interpretation of the fructification.

Apart from the slightly thinner surfaces of contact between walls of contiguous sporangia, there is no systematic thickening of the sporangial walls that would suggest an annulate dehiscence mechanism.

When viewed in transverse section, cells of the outer layer appear irregularly hexagonal in outline, with long and short transverse axes reaching 100 and 60μ, respectively (pl. 21, fig. 11); the long axes are oriented parallel with the polar axis of the sporangium. When seen in longitudinal section, these cells present a palisadelike appearance. They are heavily thickened on their outer and radial walls, the innermost walls being very thin in contrast. The lacunae are small in proportion to the outside dimension of the cells; these are shown transversely in plate 21, figure 11 and longitudinally in plate 21, figure 3 (the latter photograph shows a group of cells with exceptionally large lacunae). The possibility of a functional annulate interpretation of these heavily indurated cells meets with two outstanding difficulties: (1) Here the induration is centrifugal with the thinnest walls facing the sporangial cavity (indeed, in many instances the lacunae of the wall cells appear to open directly into the sporangial cavity), a condition directly opposite to that found in the annuli of modern ferns with their centripetally thickened cells; (2) here the indurated cells are not restricted to a clearly circumscribed portion of the sporangial wall as in modern fern annuli.

The sclerified cells of the outer sporangial layer end abruptly at the point of attachment of the sporangial pedicel without any appreciable decrease in size (pl. 21 fig. 4). This results in a circular aperture approximately 0.5 mm in diameter.

A lining of very delicate, thin-walled parenchymatous cells lies immediately beneath the outer layer of the sporangial wall. This lining reaches a thickness of about 100μ and is composed of three or four layers of flattened, platelike cells whose greatest dimensions lie parallel to the sporangial surface (pl. 21, fig. 2). In the majority of the sporangia the inner tissue is poorly preserved or entirely lacking; its remains are usually indicated by a thin membrane surrounding the spore mass (pl. 21, fig. 4). The best instances of preservation of this tissue are invariably found in the basal portions of the sporangia. There is no evidence of vascularization in this tissue.

The sclerotic cushion.—In a median longitudinal section of the sporangium (pl. 21, figs. 1, 4, 5), the sclerotic cushion appears as a conspicuously dark and wedgelike or saucer-shaped structure. Its basal portion is normally situated in a position essentially flush with the aperture in the sclerotic outer layer of the sporangial wall. It does not, however, completely fill this opening nor is it in direct connection with the latter tissue. It flares out distally and terminates in a concave distal surface that forms a direct continuity with the inner surface of the parenchymatous layer of the sporangial wall (pl. 21, fig. 1). It may reach 0.7 mm in diameter.

In some instances the sclerotic cushion has been displaced distally beyond the inner limits of the sporangial wall; this is most likely a positional distortion effected following the disorganization of the inner parenchymatous lining of the sporangium.

Individual cells of the sclerotic cushion are fusiform; in the center of the cushion, their long axes are directed parallel to the polar axis of the sporangium; but proceeding toward the margin of the cushion, they come to lie parallel with the surface of the sporangium. The cells average 80μ in length and 35μ in width. The walls are heavily thickened. Cells of the cushion differ markedly from those of the parenchyma that separates it from the sclerotic outer wall of the sporangium.

Vascular elements from the pedicel reach the proximal surface of the cushion but apparently do not penetrate into it.

The presence of this unique cushion (in sporangial fructifications) is shared only by *Mittagia seminiformis*.

The pedicel.—In only a few instances has the pedicel been observed. It is an extremely slender axis not exceeding 150μ in diameter (pl. 21, fig. 5). It contains a small vascular bundle composed of tiny scalariform tracheids that extend as far as the base of the sclerotic cushion. The extrastelar parenchyma of the pedicel is in organic connection with the soft inner tissue of the sporangial wall; whether or not the epidermis of the pedicel forms a direct continuity with the outer layer of the sporangial wall has not been determined. In the majority of cases, the sporangia are borne singly upon the pedicels; but in one instance, a bifurcated pedicel was seen with two very short termini, each bearing a sporangium at its tip.

In no instance has the pedicel been followed for more than 1 or 2 mm from the point of sporangial attachment. Numerous small axes with diarch steles are intimately associated with the fructifications. These are somewhat stouter than the pedicels and may have been the axes that produced the latter. Such an association is not demonstrable, however, nor is it possible to determine the affinities of these axes beyond the assumption that they are apparently not of stigmarian origin.

Dehiscence.—Little evidence is present concerning dehiscence of these peculiar sporangia. There is no differential development of the sporangial wall which might properly be interpreted as an annulate dehiscence mechanism comparable to those of modern ferns.

In one instance (pl. 21, fig. 10) a sporangial wall is fractured at a point near the base, and the edges are curled inward toward the sporangial cavity. This is as might be expected and may represent the normal type of dehiscence if a mechanical function may be ascribed to the centrifugal thickening of the outer cells of the sporangial wall. If so, the cumulative action of all these cells might have forced a fracture and incurling of the sporangial wall, the line of dehiscence depending upon loci of weakness in each individual sporangium.

An alternative speculation is suggested by several fragments of sporangia, varying in size, scattered through the matrix. The sclerotic outer wall of the sporangium probably became extremely brittle upon drying and was readily broken into irregular fragments upon agitation by the wind and friction with adjacent sporangia.

Spores.—The majority of the sporangial cavities are uniformly filled with essentially spherical spores that vary from 45μ to 55μ in diameter. In some instances the spores are slightly flattened on their proximal surfaces, the three facets representing surfaces of contact with sister spores of the same tetrad; no intact tetrads have been observed, however.

The spore exines are thick (reaching 5μ) and are covered with coarse reticulations of ridges that reach 3μ in height and 3μ in thickness (pl. 21, figs. 7, 9). The reticulations form a pattern of irregular polygons with essentially straight sides. They are usually most strongly developed on the distal surfaces of the spores, but in some instances they extend as far as the triradiate ridges. More usually, however, the reticulations are weakly developed or entirely lacking over the greater part of the proximal surface of the spore.

The triradiate ridges are usually faint, with little relief; their rays measure from 20μ to 25μ in length (pl. 21, figs. 6, 8).

Many of the spores contains an inner body, usually a dark spherical mass with a smooth or slightly wrinkled surface; this is quite separate from the spore exine. These bodies reach about 30μ in diameter; they may represent the shrunken remains of an inner spore membrane (pl. 21, fig. 6).

The spores seem to agree generically with *Reticulatisporites*, as redefined by Schopf, Wilson and Bentall (1944, p. 34).

Discussion.—In the structure of the sporangial wall and size of sporangia, *Sclerocelyphus* contains certain points of similarity to sporangia of the sphenophyllaceous strobilus *Bowmanites trisporangiatus* Hoskins and Cross (1943). The *Bowmanites* fructification contains a prismatic outer layer of heavily thickened cells lined by a delicate parenchymatous layer very similar to the corresponding tissues in *Sclerocelyphus*. However, the basal sclerotic cushion is a feature not present in *Bowmanites*. Furthermore, there is absolutely no evidence that *Sclerocelyphus* was part of a strobilar unit. The compactly arranged groups of sporangia (pl. 21, figs. 10, 12) are much too intimately associated to allow for any intervening strobilar appendages, had such been present. Had the sporangia been shed from a strobilus, there is little likelihood that they would have fallen into such a compact group; nor would their thinner surfaces of sporangial contact have maintained their original juxtaposition with the corresponding surfaces of contiguous sporangia. It is difficult to visualize the group of sporangia shown in plate 21, figure 10, becoming oriented with their axes all pointed in the same direction unless they grew in such a manner and were preserved in essentially their natural positions. Detached sporangia are found abundantly in coal balls. However, it is seldom that large numbers are found in close association without affording some evidence regarding the plant organs that bore them. The orientation of this particular group of sporangia suggests that they were borne much like those of *Botryopteris forensis* or *B. globosa*, in large clusters terminating the smallest ramifications of a highly branched axis, rather than in a strobilar fructification.

The only previously described fructification that compares closely with *Sclerocelyphus* is *Mittagia seminiformis* Lignier, which was originally described from Lower Silesian coal balls equivalent in age, according to Schopf (1941, p. 9), to the lowermost portion of the Morrow series of the American Pennsylvanian. A second occurrence of *Mittagia* may now be reported. A nodule collected at the Kilpatrick hills of Dunbartonshire, Scotland, from the Calciferous Sandstone series of the Lower Carboniferous by Professor John Walton, of Glasgow University, contained a single specimen, apparently referable to *Mittagia*. The specimen was kindly loaned to me by the collector. Unfortunately, the preservation is not sufficiently complete to afford additonal details to Lignier's original description of *Mittagia*. In *Mittagia* we find every distinguishing feature of *Sclerocelyphus* sporangia: the sclerotic outer wall, the delicate parenchymatous inner wall, and the sclerotic basal cushion or "cupule" of Lignier's terminology. Furthermore, the sizes of the two fructifications compare closely, and it would be difficult to distinguish differences of more than mere specific value if empty sporangia of *Mittagia* and *Sclerocelyphus* were placed side by side for comparison. Then the chief distinctions would lie in the sporangial dimensions, microscopic details of the sporangial walls, and the presence or absence of a dehiscence mechanism. While no clear-cut dehiscence mechanism is apparent in *Sclerocelyphus*, Lignier described a longitudinal line of dehiscence in *Mittagia*. It was marked by an abrupt diminution of the sclerotic cells on either side of the cleft; presumably the sporangia were two valved as a result of this mechanism.

There are more significant factors, however, which preclude any strong likelihood of congenerity between *Mittagia* and *Sclerocelyphus:*

1. Spores: *Mittagia* contains four megaspores, whereas *Sclerocelyphus* contains numerous small spores; and while *Mittagia* unquestionably represents the female fructification of a heterosporous plant, nothing is known of its microsporangiate counterpart. To infer a congenerity between the two fructifications would then necessitate the following assumptions:

(*a*) That the male and female organs of the plant that bore *Mittagia* were alike in every detail except for the differences between megaspores and microspores. This in itself is not an unreasonable assumption, in consideration of what is known about the fructifications of certain other Carboniferous heterosporous plants; but in this instance the uniqueness of the *Mittagia* fructification suggests that we may be dealing with a very unusual and perhaps entirely unknown type of plant.

(*b*) That *Sclerocelyphus* is the male fructification of a heterosporous plant whose megasporangia are identical with *Mittagia* rather than an isosporangium or the microsporangium of a seed plant. To definitely establish it as any thing other than an isosporangium will necessitate more information than that presently at hand.

2. Comparative ages: *Mittagia* is geologically much older than *Sclerocelyphus;* the type specimens originated from coal beds in the Koksflöz (Namurian series), and its geologic range is extended to the basal part of the Lower Carboniferous (lowermost Calciferous Sandstone series) by the discovery of the Scottish specimen.

3. *Associated fossils:* Although there is no need to discuss the indecisiveness of associations, it may be of some interest to point out that the floras associated with *Mittagia* and *Sclerocelyphus*, insofar as they are known, contain not a single common element. The Silesian nodules have been investigated by Kubart (1908) and Stur (1885); the flora is almost exclusively a *Lyginopteris-Heterangium* assemblage with several species of each. (See Hirmer, 1927.) Although *Lyginopteris* has been reported in American coal balls, the evidence for its presence is rather slender. Certainly it has not yet been noted in the Kansas material; *Heterangium* is not rare in American coal ball floras, but it too is yet unknown in the Kansas material.

The above factors would seem to encourage the proposal of *Sclerocelyphus* as a new genus, at least tentatively and pending further evidence pertinent to its possible relationships with *Mittagia.* The striking structural similarities between the two fructifications are beyond ascription to coincidence; indeed, they invite postulation of *Sclerocelyphus* as the male organ of a plant directly descended from that which bore *Mittagia.* Perhaps it is even the male organ of a seed bearing plant; for in consideration of the greater age of *Mittagia,* it seems reasonable that the time lapse was sufficient for the megasporangium to evolve into a bona fide seed. If such should prove to be the case, the similarity of *Sclerocelyphus* to *Mittagia* would be ascribable to "conservatism of male parts," and the generic separation of the two fructifications would be more completely justified.

The generic name *Sclerocelyphus* is proposed with reference to the sclerification of the sporangial wall and of the basal cushion (Greek skleros, tough; kelyphos, case). The specific name *oviformus* refers to the shape of the sporangia.

Generic Diagnosis.—Sporangia large, massive-walled, terminally borne on slender pedicels, probably in botryoid clusters; spores small and numerous. Sporangial wall with an outer sclerotic prismatic layer a single cell thick and an inner parenchymatous layer several cells thick. Base of sporangium containing a sclerotic cushion; vascular tissue of the pedicel reaching the base of the sclerotic cushion.

Specific diagnosis.—Sporangia ovoid to globular, with average diameters of 2 mm. Outer sclerous layer of sporangial wall composed of irregularly hexagonal palisade cells averaging 100μ by 60μ in transverse dimensions and from 40μ to 100μ in thickness, the thinnest cells occurring at points of juxtaposition with contiguous sporangia. Inner parenchymatous layer of sporangial wall averaging 100μ in thickness. Sclerotic cushion reaching 0.7 mm in diameter and composed of short (averaging 80μ in length) fusiform cells. Dehiscence mechanism not known.

Spores spherical, ranging from 45 to 55μ in diameter. Exines thick, ornamented with coarse reticulations of thick ridges; reticulations sometimes complete, sometimes absent from proximal surfaces of spores. Triradiate ridges present, the rays averaging 20μ in length. Spores sometimes containing dark inner bodies averaging 30μ in diameter and probably representing shrunken inner membranes.

Stratigraphic occurrence.—Fleming coal of the Cherokee shale (Desmoinesian series of the Pennsylvanian as classified by the Kansas State Geological Survey).

Locality.—Pittsburgh and Midway Coal Company strip pits, about 4 miles south of West Mineral, Kans. (Columbus quadrangle, Cherokee County).

Type material.—Slides 2000 to 2014, inclusive, in the Washington University paleobotanical collection. The slides were made from peels of coal ball WCB 711–B; the unmounted peels of this series are entered in the Paleozoic plant collection in the U. S. National Museum.

Tyliosperma orbiculatum Mamay, n. gen., n. sp.

Figures 2–4 and plates 22, 23.

Material.—Four specimens provide the basis for this description. Three were investigated by means of longitudinal or oblique longitudinal series, the fourth transversely. The first and most complete specimen found was encountered in coal ball WCB 711–B during the preparation of peels of the *Sclerocelyphus* specimens. It occurred in close association with the *Sclerocelyphus,* lying within a centimeter of the sporangial cluster. This specimen will be referred to as specimen *A*; it was entirely consumed in the preparation of a series of 160 oblique longitudinal peels (711–B; 100–260). The description is based largely on this specimen.

Specimens *B* (WCB 717–F, t) and *C* (WCB 717–I, t) were longitudinally exposed by the original saw cuts of the coal ball. Since approximately one-third of each was lost in the saw kerf, the peel series of these two specimens are incomplete; they do, however, substantiate the conclusions derived from specimen *A*.

Specimen *D* was exposed transversely, the apical portion lying above surface WCB 717–I, b, and the basal portion below the contiguous surface WCB 717–H, t. The saw cut consumed the major portion of the nucellar mound and the floor of the micropylar chamber; these features are clearly understood, however, from the longitudinal series of specimen *A*. Both portions of specimen *D* were entirely consumed in the preparation of peel series 717–I, b 1–22 and 717–H, t 1–17.

General morphology.—The seeds are small, simple, and radiospermic. They are nearly spherical, except for slight protrusions of the apical lobes and a slight flattening or beveling of the portion of the integument surrounding the chalaza. The seeds reach a maximum of 3.7 mm in length and 3.5 mm in diameter.

The free micropylar portion of the integument forms a canopy over the micropylar chamber; this canopy is divided into seven essentially equal lobes, which extend proximally to a level only slightly higher than that of the floor of the micropylar chamber. An undetermined number of vascular strands lie against the inner surface of the integument.

A broadly conical mound of delicate nucellar tissue extends upward into the micropylar chamber. This is closely invested by an epidermal sheath that is continuous with the epidermis of the canopy. The epidermal sheath is open at the summit, leaving the very tip of the nucellar mound exposed.

An interesting feature of the seed lies in the presence of a sclerified chalazal cushion that bears a noteworthy resemblance to the sclerotic cushions in the bases of the *Sclerocelyphus* sporangia. The basal portion of the chalazal cushion is composed largely of delicate parenchyma, supplied with vascular tissue that originates from the cupule; the bulk of the cushion is sclerified.

The cupule is a deeply lobed structure that closely invests at least the basal half of the seed; the distal extent of the lobes is not certain. The seed is sessile on the cupule; there is a direct continuity between the epidermis of the integument and that of the cupule, and between the chalazal cushion and the inner tissues of the cupule.

The integument.—The integument contains an epidermis, a single cell thick; a palisade layer, also a single cell in thickness; and an inner layer, several cells thick, which makes up the greater bulk of the integument (pl. 22, fig. 4).

The epidermis was extremely delicate; hence, it is absent from the outer surfaces of all specimens except *C* and *D*. In these it appears as a thin black line that is separated from the seed by only a very slight interval, perhaps the thickness of a single cell. In plate 23, figure 1 (a transverse section through the apical lobes of the canopy) the epidermis may be seen extending over the inner surfaces of the lobes; it is absent from their outer surfaces, however. This condition is seen in all sections made through the micropylar chamber except specimen *C*. The epidermis forms a complete lining for the chamber; it also forms the sheath that encloses the nucellar mound. The continuity of the epidermis from the inner surface of the integumental lobes to the sheath is shown in plate 23, figures 8 and 9.

Beneath the epidermis there is a palisade layer, in most parts only a single cell thick. The palisadelike arrangement of these cells is most distinct in the equatorial portions of the seed but becomes less clearly defined as the poles are approached. These cells reach maximums of 85μ in length and 55μ in diameter. They are in sharp contrast with the cells of the inner part of the integument by virtue of their cellular contents; the palisade cells contain a brownish substance (probably the remains of a mucilaginous product) that is absent in the remainder of the integument (pl. 22, figs. 4, 6). The palisade layer is not entirely restricted to the outer surface of the seed; it extends over the inner surfaces and as far as the bases of the integumental lobes. Toward the tips of the lobes, the inner and outer palisade layers tend to lose definition as such and merge into a rather homogeneous, dark tissue (pl. 23, figs. 8, 9). This coalescence is accompanied by a diminution in cell size.

The inner tissue of the integument is composed of a very homogeneous mass of parenchyma, several cells in thickness. Toward the outer surface of the integument, they are irregular in shape and arrangement, but those toward the inner surface tend to become flattened in the plane parallel to the seed surface. Although the majority of the sections leave some doubt as to whether the inner limits of the integument are preserved, other sections (especially in specimens *B* and *C;* see pl. 22, fig. 8) show the innermost layer of cells to present a perfectly smooth, undisrupted inner surface; probably this is the actual inner limit of the integument. The inner and outer layers of the integument attain a combined maximum thickness of 320μ.

The micropylar portion of the integument is deeply divided into seven discrete lobes. Details of this feature were afforded by only specimens *A* and *D;* there are seven lobes in each of these, however.

Seen in transverse section (pl. 23, fig. 1) and toward their tips, the lobes appear as a series of rather triangular structures; at this point their component cells are fairly thick walled and comprise a nearly homogeneous tissue system with dark cellular contents. Proceeding in the chalazal direction the lobes tend to assume the shape of thick crescents with slight concavities on their outer surfaces. Here the differentiation between inner and outer integumental layers becomes more evident. At this level (about halfway toward their bases) the lobes are about 600μ wide and 450μ thick. They reach lengths of nearly 1 mm.

The chalazal portion of the integument is perforated by a circular aperture approximately 1 to 1.2 mm in diameter. The integumental tissue surrounding the aperture may gently decrease in thickness toward the lip of the aperture or may bear a distinctly beveled appearance on its outer surface, as shown in plate 22, figure 5. This is probably the result of appression with the subtending cupule.

A median transverse section of the seed shows an almost perfectly circular outline (pl. 23, fig. 4). Neither ribs nor sutures are evident. However, toward the chalaza the outline assumes a roughly polyhedral aspect. In the single specimen sectioned transversely (specimen *D*), this outline appears to have seven or eight facets; an exact count is made difficult by the partial fragmentation and distortion of the specimen at this level. (See pl. 23, figs. 3 and 5.) These facets correspond with the beveling of the integument, and each probably represents the surface of contact with a single cupular lobe, although the cupule is not present in specimen *D*.

Particular attention was directed toward the vascular system, but in neither transverse nor longitudinal sections were vascular elements noted within the integumental tissues.

The micropylar chamber and nucellar mound.—By virtue of their simplicity, these features, especially the mound, stand in marked contrast with corresponding structures in other pteridospermous seeds. They are best seen in the obliquely longitudinal series of specimen *A*, which is partly represented in the series of diagrams presented in figure 2; parts of this series are also illustrated in plate 22, figures 1, 2, 3, 5, 7, and 9.

The micropylar chamber is a broadly conical cavity nearly 1 mm high and about 1.5 mm wide at the base. From the center of the floor of the chamber, a conical mound rises, which is approximately 0.5 mm broad at its base and 0.55 mm high; it terminates about 0.4 mm below the apical opening between the tips of the integumental lobes. The mound is enclosed in an epidermal sheath a single cell thick. The epidermal layer extends over the entire floor of the micropylar chamber and forms a direct continuation of the epidermal layer of the inner surfaces of the integumental lobes (pl. 23, figs. 6–9). The apex of the epidermal sheath is perforated by an opening about 0.2 mm wide (pl. 23, fig. 9). The closed appearance of the apex of the sheath as seen in figure 2, diagram *C*, is due to the obliqueness of the section, which intercepted a slight constriction below the apical aperture of the sheath.

The tissue within the epidermal sheath is an extremely delicate parenchyma that represents the apex of the nucellus. This fills the sheath nearly as far as its summit, and the tip of the nucellus is exposed only a few microns below the aperture. In a median longitudinal section the tissues of the nucellar mound and the epidermal sheath are appressed and probably are organically coalescent. This in itself presents a novel feature among pteridospermous seeds; for here the floor of the micropylar chamber, as well as the sheath of the nucellar mound, is clearly of integumental origin. This represents the highest degree of coalescence known to exist between the integument and nucellus in Paleozoic seeds.

It is possible that the specimens on hand were preserved in a slightly immature stage and that with increasing maturity the epidermal sheath became separated from the nucellar mound with the resultant cavity functioning as a pollen chamber. This is not demonstrable with the present material, however; and for this reason, in addition to the very simple structure of the nucellar mound and its enclosing sheath, I hesitate to apply the terms "pollen chamber" or "lagenostome" to any of these parts. No pollen grains have been observed within the micropylar chamber.

The nucellus.—The basal portion of the nucellus forms a conspicuous pad or cushion opposite the chalazal aperture of the integument. It has the form of a thick saucer (pl. 22, figs. 5, 7, 8); and although it is invariably somewhat displaced toward the center of the seed, the convexity of its proximal surface corresponds exactly with that of the inner surface of the integument, suggesting that it was originally tightly seated in the chalazal aperture of the integument. The cushion reaches 1.2 mm in width and 0.4 mm in thickness.

The proximal surface of the cushion consists of delicate parenchyma. The basalmost portion is made up of parenchyma and very small tracheids that are derived from the vascular supply of the cupule. The intervening tissue, which comprises the bulk of the nucellar cushion, consists of a mass of sclerous cells that compare closely in size and appearance with the sclerous elements in the basal cushion of *Sclerocelyphus* sporangia. (Compare pl. 21, fig. 4 with pl. 22, fig. 5.)

Aside from the nucellar mound and the basal cushion, the remainder of the nucellus is incompletely preserved; the peel series of specimens *A* and *C*, however, afford a certain measure of important additional information, especially with reference to the vascularization of the seed. In these series the margins of the nucellar cushion taper off into a thin layer of delicate parenchyma that extends upward and toward the base of the micropylar chamber (pl. 22, fig. 5). In large, part of this layer is badly shrunken, appearing only as a thin line of tissue remains; however, in places the organic fusion with the integument is quite apparent. Although the greater part of the nucellus that remains has shrunk away from the integument, there is little question that the two tissues were originally confluent as far as the

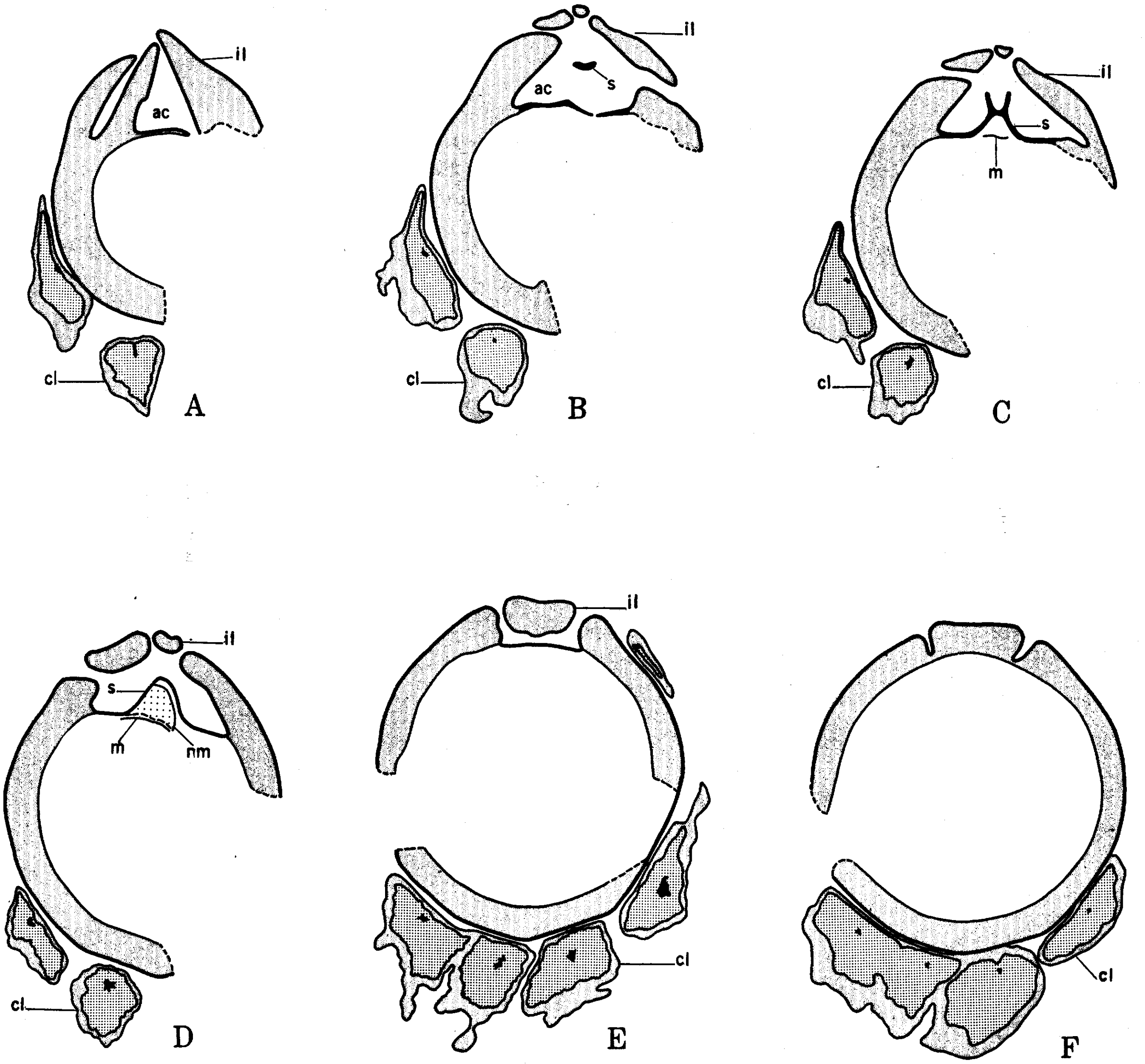

FIGURE 2.—*Tyliosperma orbiculatum* Mamay: *A* series of semidiagrammatic, camera lucida drawings of several sections from the oblique-longitudinal series of specimen *A*. *A-F*, the apical structure of the seed and lobation of the cupule. Drawings made from slides as follows: *A*, 2034; *B*, 2037; *C*, 2038; *D*, 2041 (see also pl. 2, fig. 1, and pl. 3 fig. 8); *E*, 2044 (see also pl. 2, fig. 3, and pl. 3, fig. 7); *F*, 2046.

Tissues shaded as follows:

Fine stipplings	integument of seed and compact outer layer of cupule
Medium stippling	delicate inner tissue of cupule
Coarse stippling	undifferentiated nucellar tissue
Solid-black shading	xylem
Heavy black line over surface of integument, floor of apical chamber, and nucellar mound	integumental epidermis
Cross hatching	sclerenchyma

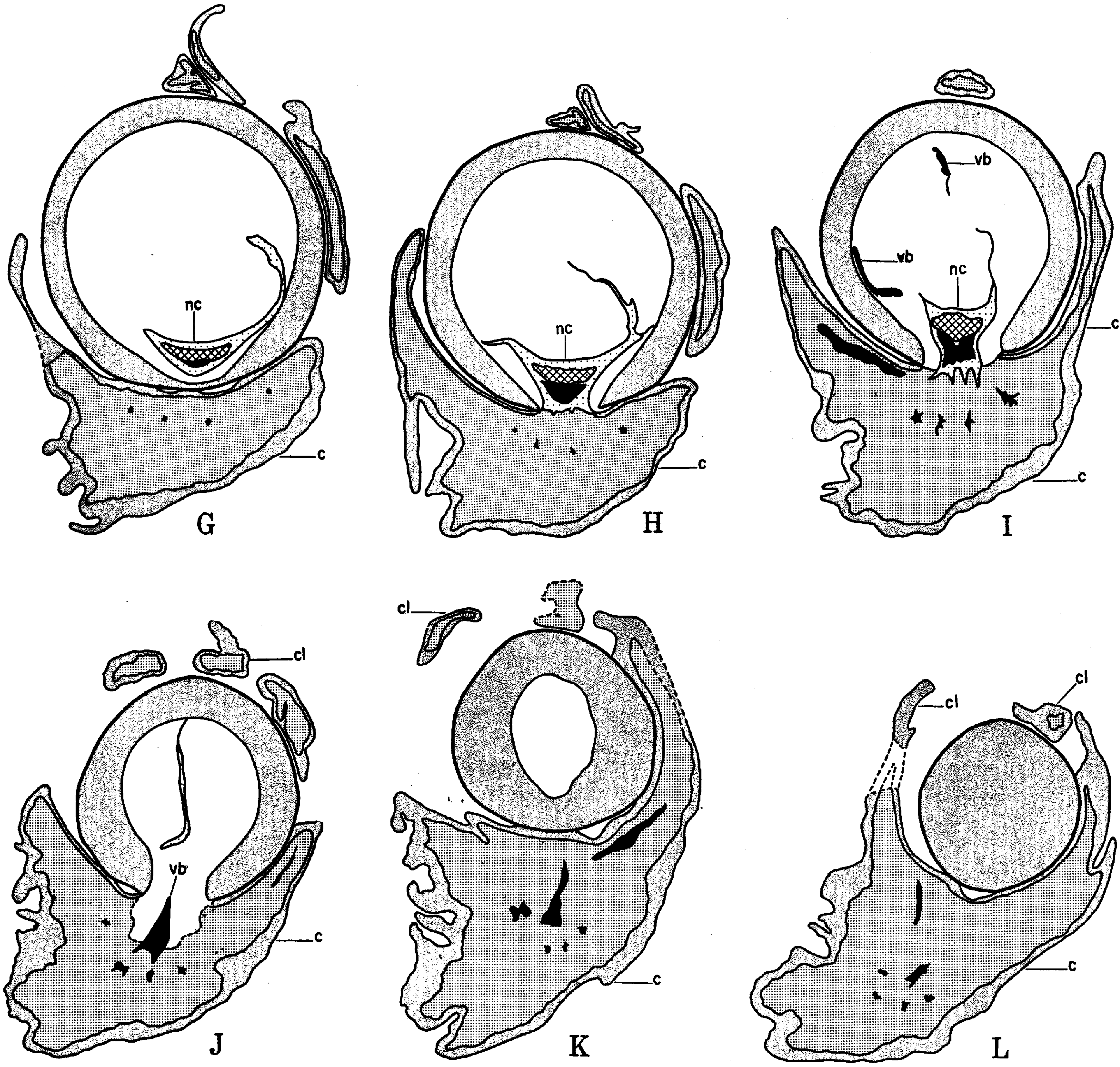

FIGURE 2.—Continued.

G-L, the basal structure of the nucellus and vascularization of the seed. Drawings made from slides as follows: *G*, 2048; *H*, 2049; *I*, 2051; *J*, 2053; *K*, 2054; *L*, 2055.

Parts lettered as follows:

ac	apical chamber
c	cupule
cl	cupule lobe
il	integumental lobe
nc	nucellar cushion
nm	nucellar mound
m	megaspore membrane
s	sheath of nucellar mound
vb	vascular bundle

tip of the nucellar mound in the micropylar chamber.

Vascularization.—Since the vascular system was not apparent in the sections of the single specimen studied in transverse section, investigation of this important feature was limited to longitudinal sections; hence, the number or disposition of the vascular bundles was not determinable, although it is apparent that the seed was fairly well supplied with conducting tissue.

The main vascular system of the cupule, a strand approximately 0.2 mm thick, enters through the chalaza into the base of the nucellar cushion (fig. 2, diagram *J*). The strand flares out toward the margins of the cushion; and narrow strands depart, proceeding distally almost as far as the base of the micropylar chamber. A few tracheids from the nucellar cushion are shown in plate 23, figure 2.

In specimen *C*, two strands arise on either side of the seed. Part of the length of one is organically attached along the inner surface of the integument; the other has been mechanically displaced from the inner surface of the integument.

Specimen *A* also shows two strands arising in essentially the same relative positions; the origin of one of these from the margin of the nucellar cushion is shown in plate 22, figure 7. The strands are limited entirely to the inner surface of the integument; close serial sections were employed throughout, and no evidence of vascular tissue within the integumental layers has been noted. Each of the individual slender strands have two or three thicknesses of tiny tracheids (pl. 22, fig. 4) which do not exceed 15μ in diameter and display closely set annular thickenings.

If, as in *Physostoma* and *Sphaerostoma*, a single strand was an accompanying feature of each of the integumental lobes in *Tyliosperma*, then we may assume that the seed contained seven vascular bundles. However, pending the discovery of more and better preserved specimens, this point will remain conjectural.

Megaspores.—Specimen *B* is the only longitudinally sectioned specimen that contains a complete megaspore membrane (pl. 22, fig. 8). This is seated upon the distal surface of the nucellar cushion. It is nearly spherical, measuring about 2 mm along its greater axis. There is a single deep fold in the apical surface, probably brought about by shrinkage. The membrane is thin, light brown, and devoid of any organic contents or distinguishing markings.

The median sections of specimen *A* (pl. 23, fig. 8) contain a fragment of a thin membrane, which extends across the base in appression with the tissues of the nucellar mound. Judging from its similarity in color and texture to the complete megaspore membrane, this thin membrane is interpreted as the remains of the apical portion of the megaspore.

The distorted outline of a megaspore may also be seen in the transversely sectioned specimen *D* (pl. 23, figs. 4, 5). In these figures the megaspore appears to contain a double membrane. The intimate contact between the megaspore and the nucellar cushion is clearly shown in plate 23, figure 5.

The cupule.—This structure is known only from specimen A. To more clearly illustrate the nature of this organ and its relation to the seed, a series of outline drawings is presented in figure 2. This series represents the more significant stages in the closely spaced series of oblique-longitudinal sections made of the specimen.

The first indication of the presence of a cupule associated with the seed was noted in the level represented by diagram *A*, in which it appears as a pair of irregularly shaped but distinct bodies lying near the basal portion of the seed. In this plane, however, the specimen is incomplete, the greater part of one side of the integument and cupule having been broken off prior to preservation. Not until several sections lower in the series does the entire specimen appear.

At a lower level (diagram *E*), four lobes are appressed to the basal part of the seed, with one extending nearly as far as the equatorial plane. At points of contact with the cupular lobes, the surface of the integument is slightly flattened. This level slightly precedes coalescence of the cupular lobes, which present rather irregular transverse sectional outlines, excepting their flattened surfaces of appression with the seed and with each other. They are roughly 0.7 mm broad and 0.9 mm thick. From their free outer surfaces, irregular tentaclelike processes proceed at random. These reach 0.7 mm in length and 0.15 mm in thickness; insofar as known, they are nonglandular (pl. 22, fig. 6).

The tissues composing the cupule lobes were apparently very soft and delicate and fall into two distinct zones (pl. 22, fig. 6). The outer zone is the better preserved; it consists of a rather compact layer two or three cells deep. The component cells are thin-walled parenchyma. This layer varies in thickness from about 80μ at points of contact with the seed to 150μ at the free surfaces of the lobes.

The inner parenchyma of the lobes is poorly preserved. At best it can only be said that this appears to have been a very loosely aggregated tissue of large, thin-walled cells, much less compact than the outer tissue layer.

A single delicate vascular strand not exceeding 100μ in diameter lies within each lobe, in a slightly eccentric position toward the seed surface (fig. 2, diagram *E*). The preservation of the vascular strands is too poor to allow investigation of the more intimate anatomical details; however, in several of the sections these are seen in longitudinal aspect, and the component tiny tracheids exhibit annular or spiral thickenings. The tracheids average 15μ in width.

At a slightly lower level in the peel series the four lobes become laterally united (fig. 2, diagram *G*); here the rim of the nucellar cushion also appears in the section. The cupule appears as a single thick pad of tissue; since this section was cut through interlobal planes on either side of the seed, it does not appear to enclose the seed to any great extent. However, in the preceding diagrams (fig. 2, diagrams *H* and *I*) additional lobes appear on either side of the seed and extend well up along the sides. The section shown in diagram *I* is of further interest in that it clearly illustrates the tenuous nature of the organic connection between seed and cupule. The nucellar cushion is sectioned in a nearly median longitudinal plane; extending downward from its parenchymatous base are the remains of a delicate tissue connecting it with the inner tissues of the cupule; the continuity between the epidermal layers of the cupule and integument may also be noted. The four vascular strands that supplied the lobes shown in diagram *E* now show a tendency to converge toward the center of the cupule. This is also illustrated in plate 22, figure 7.

Proceeding further with the series, a fifth vascular strand departs to the left, entering a lobe of the cupule (diagram *I*); the base of the chalazal cushion becomes deeper, and vascular elements are evident in it. These are short, relatively broad tracheids (50μ by 15–20μ) with delicate scalariform thickenings (pl. 23, fig. 2). They extend as far as the proximal surface of the sclerotic portion of the chalazal cushion.

A further section (fig. 2, diagram *J*) shows the cupule increasing in depth; the tips of additional lobes appear above the seed, bringing the total number of lobes to at least seven, and perhaps eight. The vascular strand at the base of the chalazal cushion now enters the inner tissues of the cupule, where it is surrounded by the individual strands that supply the lobes. This, the central strand, now continues down into the cupule and diminishes in width until it is no more than 130μ thick (fig. 2, diagram *L*). In the last section where preservation allows observation (fig. 2, diagram *L*), there is evidence of five minor strands surrounding the central one. The outline of the cupule has here increased in depth (to 3 mm) and decreased in width (to 2 mm) until it suggests a somewhat obliquely sectioned slender axis or pedicel. (See pl. 22, fig. 9.)

Unfortunately the cupule and its enclosed seed bear no distinctive features that might afford a clue as to the identity of the plant that bore them. The vascular system is too poorly preserved for determination of the anatomical structure of the individual vascular strands; likewise, details of the pitting of the xylem elements, aside from those spiral and annular thickenings mentioned in a previous paragraph, are not known. Neither the exact number of cupular lobes nor the extent to which they enclosed the seed are known.

In spite of these gaps in our knowledge of this organ, the cupule remains important in that it definitely establishes the cupulate nature of *Tyliosperma*, a feature that has been previously demonstrated in *Lagenstoma*, *Gnetopsis*, and *Sphaerostoma* but only surmised in connection with *Conostoma* and *Physostoma*. The cupulate nature thereby supports the proposal of a lagenostomalian affinity for *Tyliosperma*. Indeed, the cupule itself bears a marked resemblance to that of *Lagenostoma lomaxi*, differing only in minor details. The cupule of *Tyliosperma* is more deeply lobed, lacks glandular emergences, and apparently does not enclose the seed as completely as that of *Lagenostoma*.

A reconstruction of *Tyliosperma* and its cupule, based on the series of sections of specimen *A*, is presented in figure 3. Although the length of the cupular lobes is not definitely known, I believe this to be a fairly accurate restoration of the general external aspect of *Tyliosperma*. The reconstruction is supplemented by figure 4, a partially restored, diagrammatic longitudinal section of the seed and cupule.

Comparison with other Paleozoic seeds.—The fundamental organizational features of *Tyliosperma* (its radial symmetry, the apparent cohesion between nucellus and integument, and the structure of the micropylar region) as well as its cupulate nature suggest affinity with the Lagenostomales as defined by Seward (1917, p. 308). It is, however, sufficiently unique in several details that its reference to any of the previously described seed genera included in this group is clearly unwarranted.

The deep lobation of the integumental canopy itself affords grounds for a generic separation of *Tyliosperma* from *Lagenostoma* Williamson, *Conostoma* Williamson, *Gnetopsis* Renault, and the recently described *Coronostoma* Neeley (1951); all of the these genera possess unlobed integuments. The peculiar plumelike apical processes of *Gnetopsis* as well as the presence of several seeds in a single cupule lend additional weight to an already clearcut distinction from *Tyliosperma;* indeed, in these features *Gnetopsis* stands quite apart from any lagenostomalian entity. *Conostoma*, *Coronostoma*, and *Lagenostoma*, on the other hand, share the distinctive feature of a complex pollen receiving mechanism, the lagenostome, by virtue of which they cannot be confused with *Tyliosperma*, in which the lagenostome is lacking.

While the remaining lagenostomalian genera, *Physostoma* Williamson and *Sphaerostoma* Benson, resemble *Tyliosperma* in their lobed integumental canopies, they

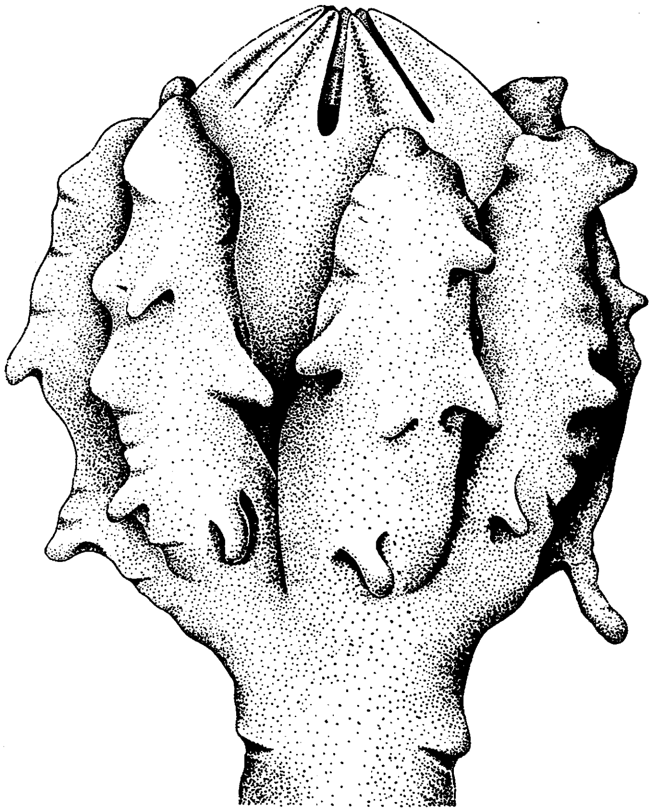

FIGURE 3.—Reconstruction showing the external aspect of *Tyliosperma orbiculatum* and its cupule.

contain important differences from the latter genus. The circumscissile dehiscence of the pollen chamber of *Sphaerostoma*, the retention of an epidermal covering on the apex of the nucellar central column (the nucellar mound of *Tyliosperma*), and the projection of the megaspore into the nucellar apex of *Physostoma* are features whose absence in *Tyliosperma* provide grounds for generic separation.

Further distinguishing features among these three genera are to be found in their chalazal regions and vascular systems. The conspicuous sclerotic nucellar cushion of *Tyliosperma* has no counterpart in either *Physostoma* or *Sphaerostoma*. Furthermore, while these two genera contain vascular systems that are well imbedded within their integuments, the vascularization of *Tyliosperma* is clearly of nucellar origin and has not been observed to penetrate into the tissues of the integument, although it does lie appressed against the inner surface of the latter.

In the light of the comparisons presented, the creation of a new genus for this uniquely simple seed seems to be in order. The generic name *Tyliosperma* (Greek tyleion, cushion, bolster; sperma, seed) is proposed, with reference to the conspicuous nucellar pad or cushion, which constitutes one of its more outstanding distinguishing characters. The specific name *orbiculatum* refers to the shape of the seed.

Generic diagnosis.—Seeds small, radiospermic, borne sessile in lobed cupules. Integument unribbed, apparently nonvascularized; free apical portion forming a deeply lobed canopy over the micropylar chamber, basal portion with a circular chalazal perforation. Micropylar chamber completely lined by an epidermal layer continuous with that of the integumental lobes.

Nucellus fused with integument; all vascular tissue apparently of nucellar origin. Basal portion of nucellus forming a conspicuous cushion; apical portion projecting into the micropylar chamber as a simple mound, encased in a sheath formed by the epidermis of the micropylar chamber, except for an apical perforation.

Specific diagnosis.—Seeds ovoid to spherical, reaching 3.7 mm in length and 3.5 mm in diameter. Integument to 0.35 mm in thickness, composed of a simple epidermis one cell thick, a palisade layer one cell thick with dark-brown cellular contents, and a thick inner fleshy layer. Lobes of integumental canopy to 0.9 mm in length, seven in number.

Nucellar cushion to 1.2 mm in width, 0.4 mm in thickness; cells of innermost portion of the nucellar cushion heavily sclerified. Base of cushion receiving a supply of small xylem elements from the cupular

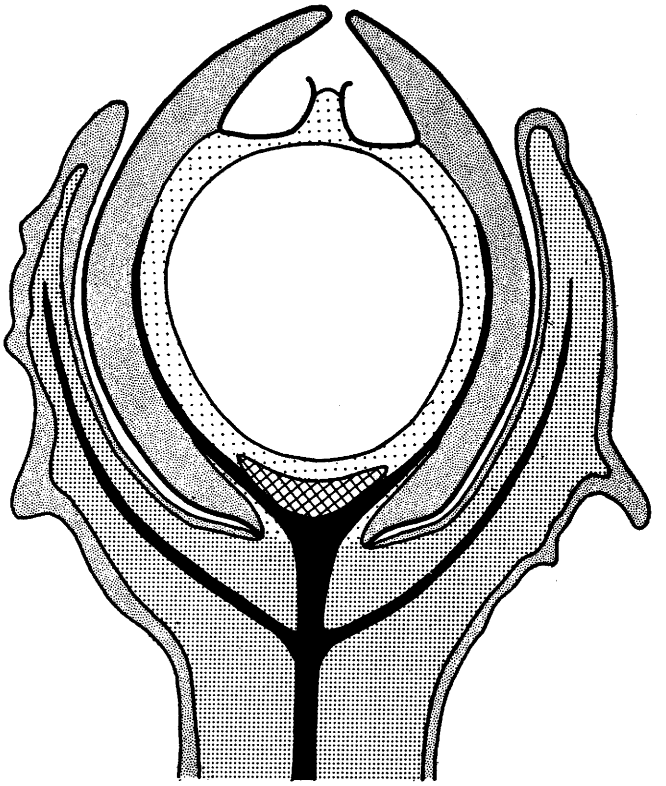

FIGURE 4.—Partially restored semidiagrammatic median longitudinal section of *Tyliosperma orbiculatum* Mamay. Shading as in figure 2.

vascular system; vascular strands (number unknown) departing from margin of the nucellar cushion, proceeding in the apical direction and appressed against the inner surface of the integument. Apical mound of the nucellus 0.55 mm wide at the base, 0.5 mm high, terminating well below the micropylar opening of the integument.

Cupule divided nearly as far as the base of the seed into seven, possibly eight thick, fleshy lobes; apical extent of the lobes uncertain. Lobes to 0.9 mm thick and 0.7 mm wide; irregular nonglandular processes produced on free outer surfaces of lobes. Each lobe containing a single, small, vascular strand. Extravascular tissues delicate, undifferentiated. Basal portion of cupule tapering into a thick, fleshy pedicel.

Microspores, vegetative parts unknown.

Stratigraphic occurrence.—Fleming coal of the Cherokee shale (Des Moines group of Pennsylvanian age).

Locality.—Pittsburgh and Midway Coal Company strip pits, about 4 miles south of West Mineral, Kans. (Columbus quadrangle, Cherokee County).

Type material.—The following slides in the Washington University paleobotanical collection made from peel sections of coal ball surfaces: WCB 711–B (specimen *A*); WCB 717–F, t (specimen *B*); WCB 717–I, t (specimen *C*); WCB 717–I, b (specimen *D*, apical portion) and WCB 717–H, t (specimen *D*, basal portion); 2015–2021 (specimen *C*); 2022–2031 (specimen *D*); 2032–2060 (specimen *A*); 2061–2062 (specimen *B*). Unmounted peels of these series are entered in the Paleozoic plant collections in the U. S. National Museum.

MORPHOLOGICAL AND SYSTEMATIC CONSIDERATIONS

In consideration of the distinctness with which *Sclerocelyphus* stands apart from all other known American Pennsylvanian fructifications, the problem of attempting to draw conclusions concerning its affinities may be approached only with extreme caution. In preceding pages certain evidence bearing against the probability of a strobilar origin of these sporangia has been presented; thus, there is serious doubt cast upon the possibility that *Sclerocelyphus* represents the fructification of any of the lycopods, articulates, or cordaitaleans, insofar as these groups are presently understood. The solitary terminal manner in which the sporangia are borne would also seem to preclude their assignment to either the Marattiaceae with their superficial synangial fructifications or to the pteridosperms with their complex synangial microsporangiate fructifications.

The manner in which the sporangia are borne in itself suggests affinity among the coenopterids, for it is chiefly within this vaguely defined and poorly understood group that terminally borne sporangia are to be found. The massive exannulate sporangial walls of *Sclerocelyphus*, however, discount an alliance with the botryopterids, whose sporangia possess a strikingly leptosporangiate aspect in their delicate annulate sporangial walls (Mamay, 1950, p. 416–417).

A somewhat closer comparison might be drawn with the fructification of *Stauropteris oldhamia;* however, the differences in detail are great, and the presence of vegetative remains of *Stauropteris* in American coal balls has not been convincingly illustrated.

There are, however, coenopterid elements in the Kansas flora whose fructifications remain unknown; *Etapteris*, *Ankyropteris*, and *Tubicaulis* have been noted in these coal balls, and the possibility that one of these genera bore *Sclerocelyphus* cannot be discounted entirely.

If, on the other hand, the notable structural similarities between sporangia of *Mittagia* and *Sclerocelyphus* may be construed as indicative of natural affinity, then *Sclerocelyphus* must be interpreted as a microsporangium rather than the fructification of a homosporous plant.

As pointed out by Seward (1917, p. 63), histological details of the sporangial wall of *Mittagia* bear a close resemblance to those of the integument of *Lagenostoma lomaxi*. Led by this resemblance, Lignier interpreted his first specimen of *Mittagia* to be a *Lagenostoma;* the error of this identification was brought to light by the subsequent discovery of additional material that proved *Mittagia* to be a megasporangium containing four megaspores.

The sporangial wall of *Sclerocelyphus* bears an equally striking resemblance to the integument of *Lagenostoma lomaxi;* this may be demonstrated by a comparison of plate 21, figure 2 with Oliver and Scott's (1904) plate 5, figure 11.

A second and perhaps more curious point of resemblance between *Sclerocelyphus*, *Mittagia* and certain of the lagenostomalian seeds lies in their basal structures. The sclerotic cushions of *Sclerocelyphus* and *Mittagia* are disturbingly similar to the nucellar cushions of both *Lagenostoma* and *Tyliosperma;* this comparison is especially notable between *Sclerocelyphus* and *Tyliosperma*. (Compare pl. 21, fig. 4 with pl. 22, fig. 5.)

If these two points of structural similarity between a possible microsporangium (*Sclerocelyphus*), megasporangium (*Mittagia*), and seed (*Tyliosperma*) are to be interpreted as homologies, we are faced with two possibilities in morphological interpretation, the second one involving a radical departure from the tenets of accepted seed morphology:

1. That *Sclerocelyphus* is the male fructification of a

pteridosperm, and *Mittagia* represents an archaic megasporangium that eventually gave rise to a bona fide seed.

2. That the seed in some instances may merely represent a highly modified megasporangium whose integument has not been derived from an extrasporangial source but represents the original megasporangial wall. Such a conjecture has been offered by Andrews (1949, p. 493) in connection with the morphology of *Nucellangium glabrum;* he wrote:

> Can it be that we are dealing with a plant in which the protective function of the integument was developed by the sporangium wall, that is, the tissue that would normally have evolved into a nucellus of the more usual type?

While it is indeed fascinating to indulge in the consideration of morphological propositions such as those presented, they are admittedly of a highly speculative nature, and a much more complete fossil record is needed for their satisfactory support. These propositions do not surmount the evolutionary difficulties entailed in producing the complicated apical structure of lagenostomalian seeds by modification of a single simple megasporangium. Nor do they compromise the organizational simplicity of *Sclerocelyphus* with the complex synangial organization of the pteridosperm male fructifications as we know them. The question of natural affinities of *Sclerocelyphus* cannot, then, be satisfactorily answered.

In *Tyliosperma* we have a seed entailing two principal points of interest: its cupulate nature and its simplicity of structure. The cupule adds little to our knowledge of Paleozoic seed cupules; it differs from that of *Lagenostoma lomaxi* only in minor details. It is, however, the first reported occurrence of this organ in American coal ball literature; the single specimen described here reveals the delicate nature of both the cupule itself and of the attachment between cupule and seed, thus explaining the rarity of such occurrences in the fossil record.

Several points in the structure of *Tyliosperma* present striking contrasts with other lagenostomalian seeds by virtue of their simplicity. Beginning with the integument, its apparently nonvascularized and relatively undifferentiated nature is unique. Furthermore, the deeply lobed canopy, a feature previously unknown among American pteridospermous seeds, presents an extremely simple aspect. In the light of Benson's (1904) synangial theory of the evolution of seeds, Oliver (1909) has interpreted the canopy of *Lagenostoma* as an advanced state of fusion of originally free integumental lobes. If we apply this interpretation to *Tyliosperma,* it appears to occupy a primitive position among the Lagenostomales along with *Physostoma* and *Sphaerostoma.* This would necessitate the interpretation of the integument of *Tyliosperma* as originating from a partially sterilized synangium, rather than from the wall of a single megasporangium. If, on the other hand, we choose to interpret the similarities between *Mittagia, Sclerocelyphus,* and *Tyliosperma* as evidence in support of Andrews' conjecture, then the free apical lobes of *Tyliosperma* may be explained as apical proliferations of the megasporangium wall. The continuity of integumental tissue over the surface of the micropylar chamber and nucellar mound would seem to be in support of such an interpretation. If the evolutionary tendency in this case, as in so many other demonstrable instances in the plant kingdom, leads to fusion of free parts, then the freedom of the lobes of *Tyliosperma* may be interpreted as indicative of a relatively primitive condition, although by no means the archaic one.

The apex of the nucellus in *Tyliosperma* deserves careful consideration, for herein lies an important point of contrast with other lagenostomalian entities. In the latter seeds, the pollen receiving mechanisms or lagenostomes are interpreted as entirely nucellar in origin, the coalescence of nucellus and integument extending only as far as the base of the micropylar chamber. The nucellar apex thus represents a highly modified structure. In *Tyliosperma,* on the other hand, the nucellar apex forms a simple, unmodified mound of tissue. The epidermal sheath surrounding it is apparently an integumental layer; thus, if this structure be interpreted as a simple pollen chamber or lagenostome, it represents one composed of a combination of both integumental and nucellar tissues rather than only a modified nucellar apex. Accordingly, this entails a much greater degree of nucellar-integumental coalescence than that present in the related seeds. These features add to the primitive aspect of *Tyliosperma*; along with the apparently nonvascularized, relatively undifferentiated integument and the deeply lobed canopy, they lend the impression that we are dealing with perhaps one of the most primitive pteridospermous seeds discovered thus far.

The affinities of *Tyliosperma* with the pteridosperms pose a perplexing problem. To attribute a lagenostomalian affinity to it does not seem unreasonable. Its gross organization and the nature (indeed the mere presence) of its cupule support such an alliance. However the simple nucellar apex, nonvascularized integument, exclusively nucellar source of vascular tissue, and high degree of coalescence between nucellus and integument stand in discord with Seward's concept of the Lagenostomales and suggest a necessity for expansion of that concept.

Little more can be said regarding the affinities of *Tyliosperma.* While its simplicity is of considerable morphological interest and while it may possibly lead to significant new points in our understanding of the early seed plants, *Tyliosperma* cannot yet be linked with any of the presently known pteridospermous stem or foliage genera. Rather, it adds another organ genus to the overall picture of American coal ball floras and contributes to the confusion produced in dealing, as the paleobotanist must, with detached plant parts.

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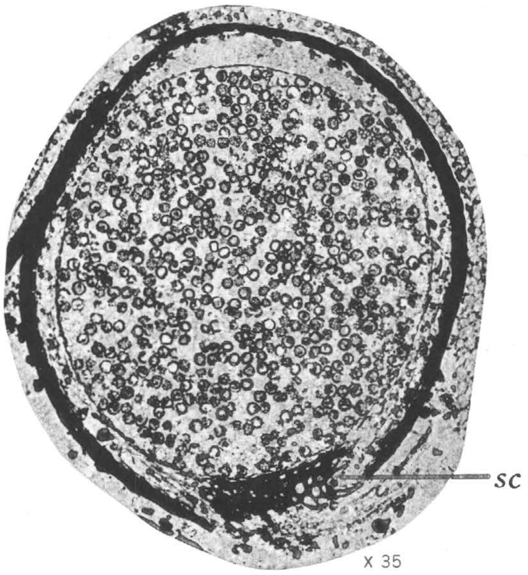
PLATES 21–23

PLATE 21

[*l*, lacuna; *p*, pedicel,; *pw*, parenchymatous inner layer of sporangial wall; *sc*, sclerotic cushion; *sw*, sclerotic layer of sporangial wall.]

FIGURES 1–12. *Sclerocelyphus oviformus* Mamay, n. gen., n. sp.

1. Longitudinal section of a sporangium, showing the sclerotic cushion and its organic continuity with the soft parenchymatous inner tissue of the sporangial wall.
   Slide 2011.
2. Section of the sporangial wall, showing the sclerotic outer layer and the parenchymatous inner layer.
   Slide 2002.
3. Longitudinally sectioned portion of the sporangial wall, showing large lacunae in the cells of the sclerotic layer. Lacunae open toward the spore cavity.
   Slide 2005.
4. Median longitudinal section of a sporangium. The sclerotic cushion has been somewhat displaced toward the inside of the sporangium.
   Slide 2007.
5. Longitudinally sectioned sporangium, showing its attachment to a pedicel.
   Slide 2013.
6. Two spores, one showing the triradiate ridge and a reticulate proximal surface; the other contains a dark inner body, probably representing a shrunken endospore.
   Slide 2012.
7. Spore, showing the characteristic reticulate ornamentation of the exine. The elliptical shape is atypical.
   Slide 2012.
8. Proximal surface view of a spore. Note the triradiate ridge and the relatively smooth proximal surface.
   Slide 2012.
9. A more typically spherical spore.
   Slide 2012.
10. Group of nine longitudinally sectioned sporangia, all oriented in the same direction. Note the fractured and inwardly curled wall of the sporangium at the lower left.
    Slide 2013.
11. Group of transversely sectioned cells of the sclerotic layer of the sporangial wall. Note the hexagonal cell outlines and the lacunae in cells toward the center of the group.
    Slide 2014.
12. Group of closely appressed sporangia, shown in transverse section. Note that the sporangial walls are thinnest at surfaces of contact with contiguous sporangia.
    Slide 2001.



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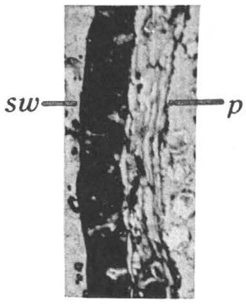

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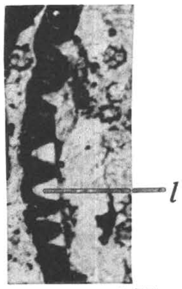

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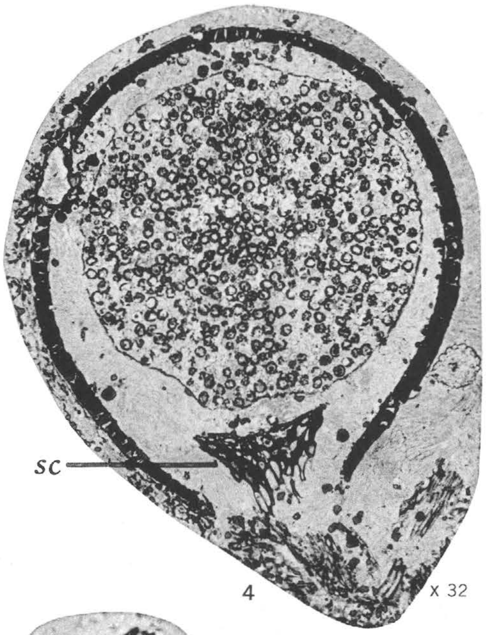

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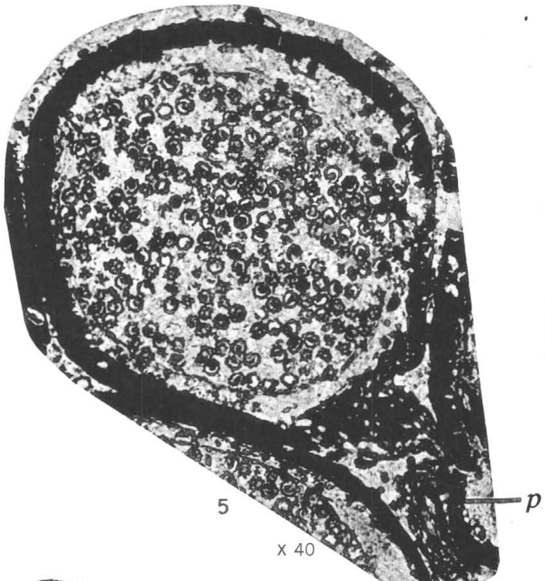

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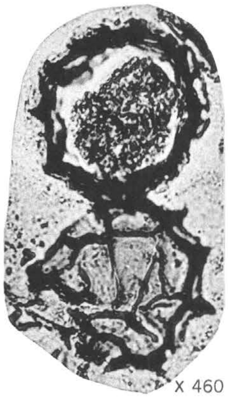

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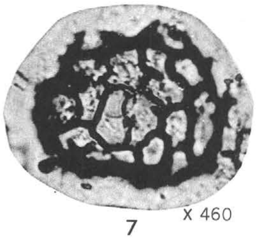

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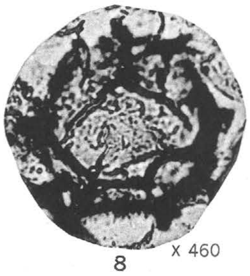

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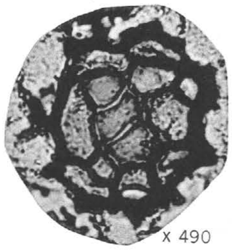

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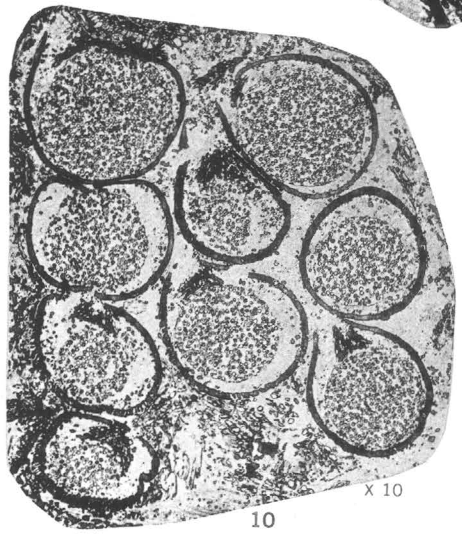

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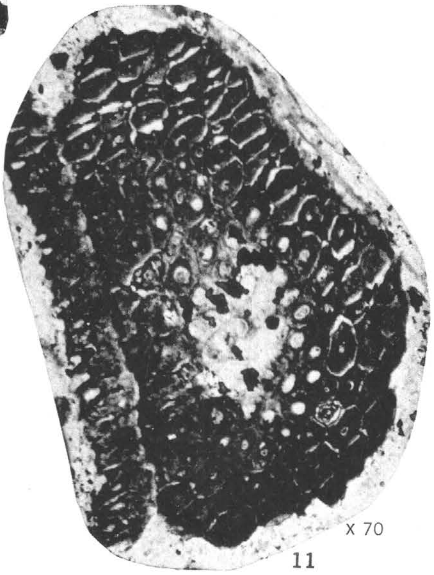

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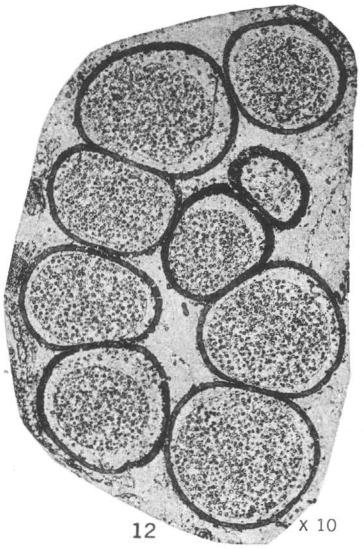

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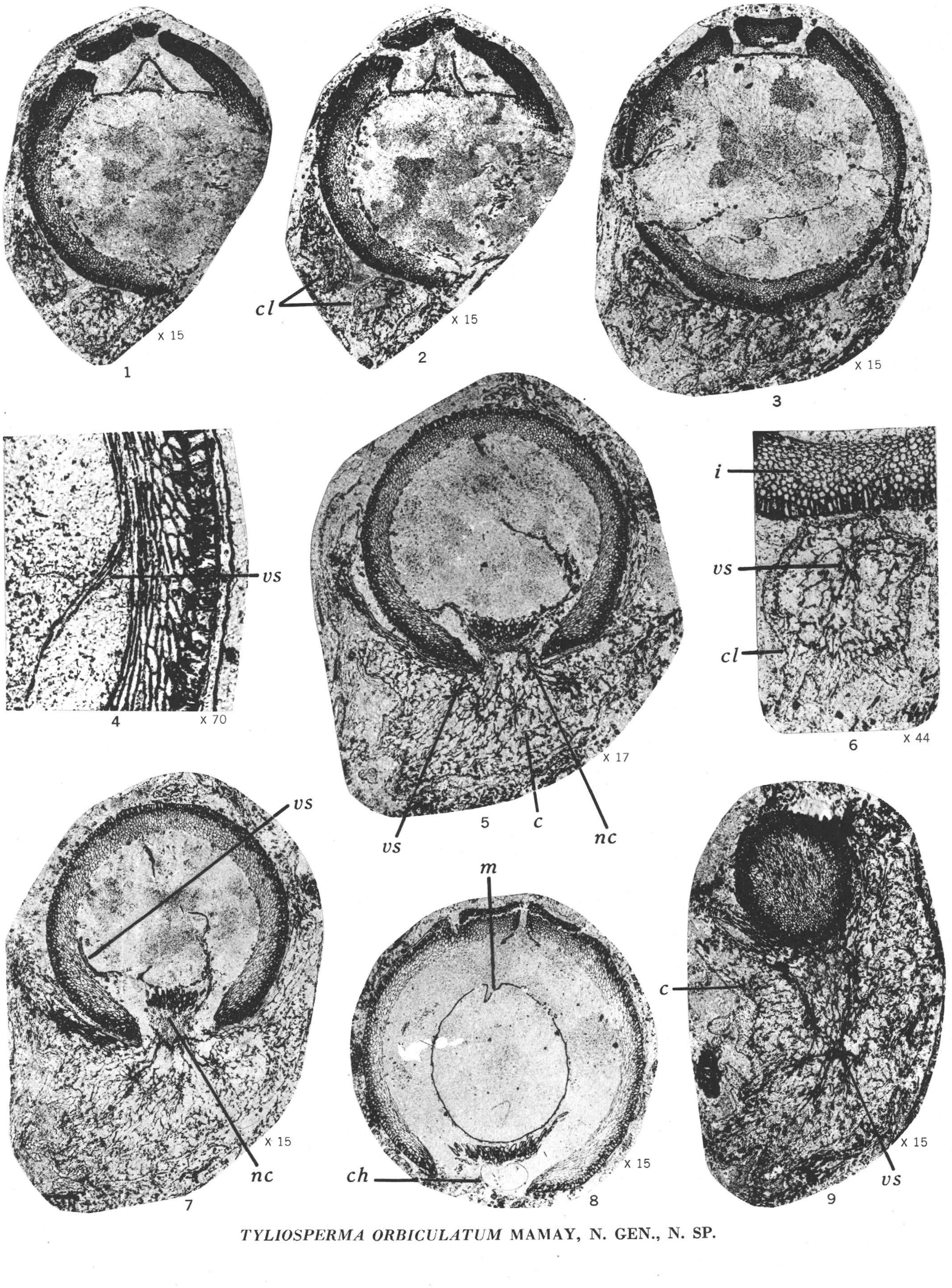
SCLEROCELYPHUS OVIFORMUS MAMAY, N. GEN., N. SP.



TYLIOSPERMA ORBICULATUM MAMAY, N. GEN., N. SP.

PLATE 22

[*c*, cupule; *ch*, chalazal aperture; *cl*, cupule lobe; *i*, integument; *m*, megaspore; *nc*, nucellar cushion; *vs*, vascular strand.]

FIGURES 1–9. *Tyliosperma orbiculatum* Mamay, n. gen., n. sp.

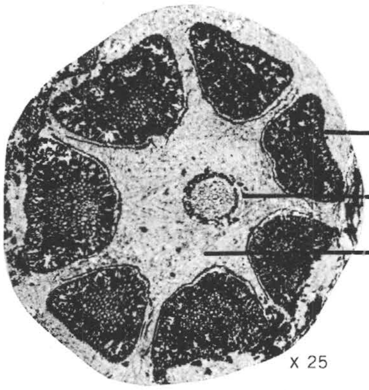
1. Oblique-longitudinal section of specimen *A*, slightly tangential to the nucellar mound. The apical portion of this section is shown enlarged in plate 23, figure 8. Successively deeper sections in this series are shown in figures 2, 3, 5, 7, and 9.
   Slide 2041.
2. A slightly deeper section than that shown in figure 1. Two lobes of the cupule are shown at the lower left. The apical portion of this section is shown enlarged in plate 23, figure 9.
   Slide 2040.
3. A slightly deeper section than that shown in figure 2. Four lobes of the cupule are shown; lateral fusion of the lobes has begun. The apical portion of this section is shown enlarged in plate 23, figure 7.
   Slide 2044.
4. Section of the integument. The epidermis is seen as a thin black line at the right. Note the palisade layer, the fleshy inner layer, and the narrow vascular strand, which has been partly torn away from its natural position against the inner surface of the integument.
   Slide 2019.
5. A slightly deeper section than that shown in figure 3. Note the sclerified portion of the nucellar cushion. Remnants of the nucellus are shown extending away from the margins of the cushion. The cupule appears here as a thick pad of tissue, with fragments of two lobes extending upward at each side of the seed. Four small vascular strands are shown in the cupule.
   Slide 2050.
6. Single lobe of the cupule, closely appressed against the integument of the seed. Note the distinct palisade layer in the integument. The loosely aggregated inner tissue, the more compact outer layer, the small vascular strand and irregular nonglandular protuberances on the outer surface of the cupule lobe are shown.
   Slide 2042.
7. A slightly deeper section than that shown in figure 5. That part of the nucellar cushion below the sclerified zone contains vascular elements. Part of a vascular strand is shown against the inner surface of the integument at the left.
   Slide 2051.
8. Tangential-longitudinal section of specimen *B*, showing the megaspore seated on the nucellar cushion.
   Slide 2061.
9. Tangential section taken just below the surface of the integument of specimen *A*. Note the irregular protuberances arising from the surface of the cupule. The vascular bundle indicated by the guide line is the main strand of the cupule; it is surrounded by several lateral strands, each of which supplies one lobe of the cupule.
   Slide 2056.

PLATE 23

[*ac*,apical chamber; *ie*,integumental epidermis; *il*,integumental lobe; *m*,megaspore; *nc*,nucellar cushion; *nm*,nucellar mound; *s*,sheath of nucellar mound.]

FIGURES 1–9. *Tyliosperma orbiculatum* Mamay, n. gen., n. sp.

1. Transverse section through the apical chamber of specimen *D*, showing the seven discrete lobes of the integumental canopy, and the nucellar mound in the center. Slide 2029.
2. Group of small annular tracheids from the nucellar cushion of specimen *A*. Slide 2051.
3. Basal transverse section of specimen *D*, showing the nucellar cushion and the faceted outline of the seed. Slide 2025.
4. Nearly median transverse section of specimen *D*, showing the megaspore membrane. Slide 2028.
5. Transverse section of specimen *D*, about midway between the sections shown in figures 3 and 4. Slide 2026.
6. Tangential-longitudinal section of specimen *A*, taken near the base of the canopy. The integumental epidermis is clearly shown. Slide 2021.
7. Enlargement of the apical portion of the section shown in plate 22, figure 3. Note the continuity of the integumental epidermis over the floor of the apical chamber. Slide 2044.
8. Enlargement of the apical portion of the section shown in plate 22, figure 1, showing the nucellar mound with its epidermal sheath. A fragment of the megaspore is also shown. Slide 2041.
9. Enlargement of the apical portion of the section shown in plate 22, figure 2. The aperture at the summit of the sheath of the nucellar mound is shown. Slide 2040.



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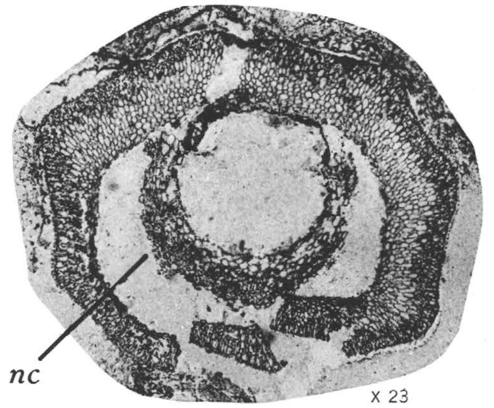

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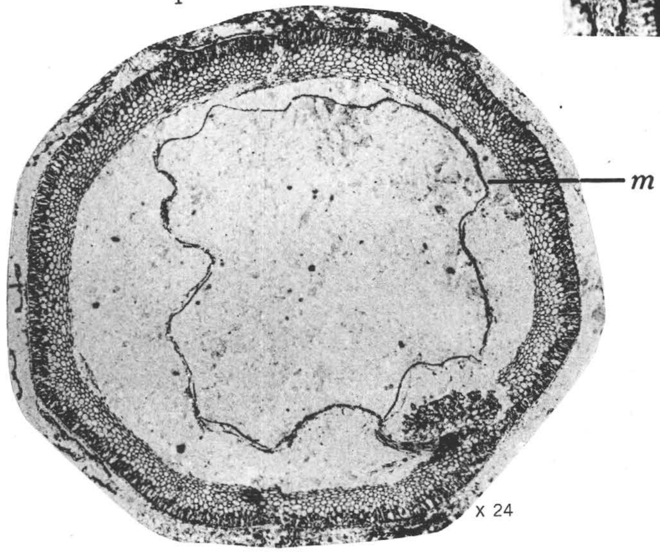

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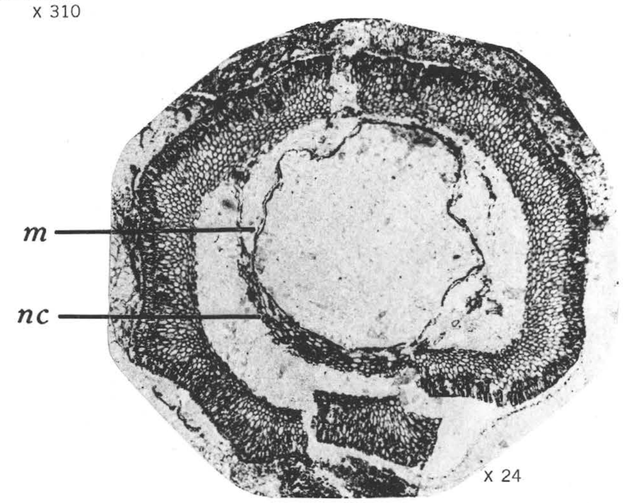

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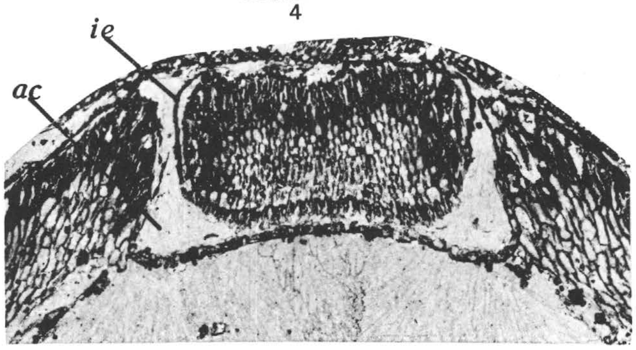

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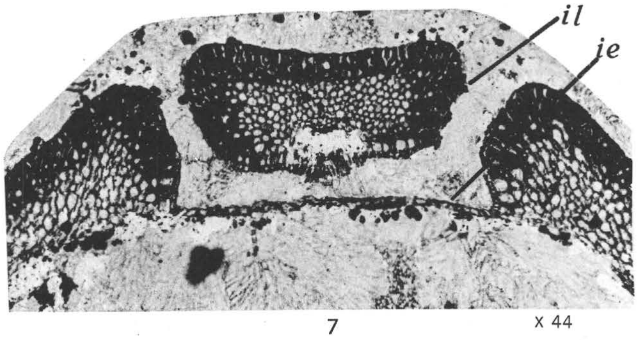

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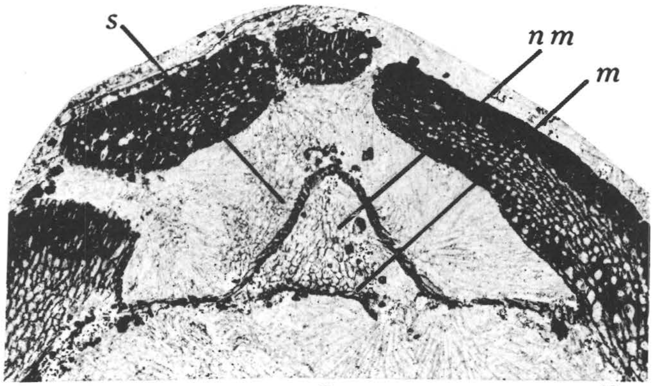

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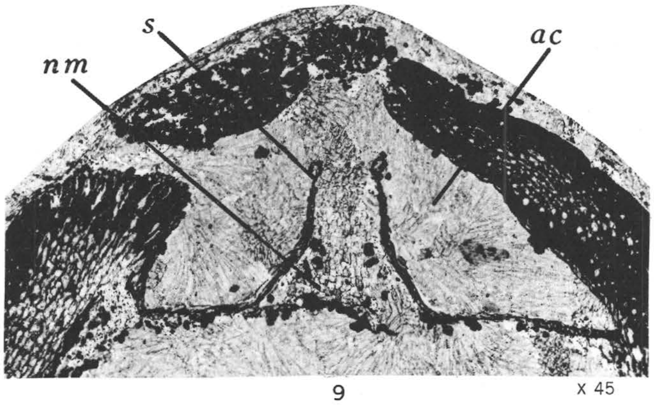

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TYLIOSPERMA ORBICULATUM MAMAY, N. GEN., N. SP.