# ONTOGENY OF *VESICASPORA*, A LATE PENNSYLVANIAN POLLEN GRAIN

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ABSTRACT. Pollen assignable to *Vesicaspora* Schemel, in spite of its conifer-like structure, is cycadophytic (pterido-spermous). It has been found *in situ* in a sporangium referable to a seed-fern, the stem of which is *Callisto-phyton*, in a coal ball of late Pennsylvanian age from Illinois. The mature pollen is monosaccate, having a saccus which is continuous equatorially, and two only slightly inflated bladders in the distal region. An onto-gentic series has also been found. The young pollen occurs mostly in decussate tetrads. A gaping sulcus develops on the distal face. Sculpture of the young pollen appears foveolate. As the saccus enlarges separation of the ektexine and endexine appears to occur. Lumina enlarge internally, especially in the bladders. In the region of the cap and the sulcus the original foveolate sculpture seems to be retained. The saccus does not extend over the cap region.

THE pteridosperm pollen organ *Callandrium callistophytoides* has recently been de-scribed by Stidd and Hall (1970*a*) from the Upper Pennsylvanian of Illinois. Its sporangia are grouped into synangia reminiscent of those of *Scolecopteris*, i.e. they are radially symmetrical, attached to a low cushion of cells, and obovate to nearly elliptical in longi-tudinal outline (Pl. 77, figs. 1, 2). Usually, there are 6 sporangia per synangium and each fertile pinna bears only one abaxial pair of synangia at the end of a dichotomizing vein. A number of anatomical and morphological features of these synangia suggests associa-tion with the stem *Callistophyton poroxyloides* Delevoryas and Morgan. The pollen in the pollinangia (a term coined by Remy and Remy 1955) is referable to *Vesicaspora*; Stidd and Hall (1970*a*) briefly mentioned the occurrence of an apparent developmental sequence of these grains. Mature pollen of *Vesicaspora* comparable to that found in the pollinangia of *Callandrium callistophytoides* has been found also by Stidd and Hall (1970*b*) in the micropyle and pollen chamber of the small seed *Callospermarion pusillum* Eggert and Delevoryas. Again, on morphological and anatomical evidence, Stidd and Hall (1970*b*) have demonstrated that this seed can also be associated with *Callistophyton*. Because of a number of unique characteristics in both seed and pollen organs, they have erected a new family Callistophytaceae, coordinate with the Lyginopteridaceae and Medullosaceae.

One striking difference between the Callistophytaceae and the other two families is the occurrence of bladdered pollen. There is no reason to suppose that *Vesicaspora*, as previously defined, occurs only in pteridosperm pollinangia, though Millay and Eggert (1970) have found it in a superficially *Cyathotrachus*-like synangium which they call *Idanothekion*. Saccate pollen does occur in other Palaeozoic pteridosperm fructifications (Remy 1953); many later-occurring Mesozoic pteridosperms also have saccate pollen (Townrow 1962).

Aside from its occurrence *in situ*, *Vesicaspora* has a widespread distribution in the dispersed state. It occurs in the Pennsylvanian and Permian in many parts of the globe (Hart 1965). The type species, *V. wilsonii* Schemel, occurs in the mid- to late Pennsyl-vanian of Iowa and Illinois (Kosanke 1969, Peppers 1970). Our material is from the

well-known coal ball locality at Berryville, Illinois (Stidd and Hall 1970*a*), in the Cal-
hoon coal, Mattoon Formation, of Late Pennsylvanian age. The material is petrified and
well-preserved, but does not seem to be *V. wilsonii*, the only species thus far recorded
from Illinois, nor is it the same as the material of *Vesicaspora* found in the sporangia of
*Idanothekion* by Millay and Eggert (1970).

*Vesicaspora* is interpreted as being monosaccate by some (Schemel 1951, Wilson and
Venkatachala 1963), bisaccate by others (Hart 1965, Jizba 1962, Clapham 1970).
Kosanke (1969) has attempted to reconcile these two viewpoints in his statement that
'if oppositely placed bladders are united even by a thin equatorial connection, a mono-
saccate condition exists'. These differences in interpretation seem to depend in part on
how the saccus is defined. It seems to us that this has been done in two ways. Erdtman
(1954) relates the number of sacci to their relationship with the surface of the corpus,
i.e. the floor of the sacci is the surface of the corpus, the number of saccale areas being
determined by the number of divisions of the corpus surface. Others use the term saccus
only for the inflated lateral or, in the case of *Vesicaspora*, mostly distal protuberances.
Thus, Clapham (1970) who considers *Vesicaspora* bisaccate, says of *V. schemelii* Klaus
that 'lateral extensions of sacci may be as wide as the greatest inflation of the saccus;
this species is distinguished from monosaccate spores by the lesser degree of inflation
of the lateral portion of the sacci'.

If one distinguishes between a saccus *sensu lato* as that bladder-like structure whose
outer wall is free of contact from the corpus, and a saccus *sensu stricto* as a protuberance
in the saccale areas, the two interpretations of *Vesicaspora*, as mono- or bisaccate, may
be explained. In our opinion, however, it is inconsistent to make this distinction. In
*Schulzospora* Kosanke there is a saccus *s.l.*, but no sacci *s.s.*; yet, in terms of the con-
figuration of this structure alone, *Vesicaspora* differs only in having two distal protuber-
ances flanking the sulcus, these being the sacci *s.s.* Thus, we agree with Kosanke's (1969)
and Erdtman's (1954) interpretation of the saccus, in which case *Vesicaspora* is mono-
saccate. Even so, it must be admitted that it is sometimes difficult to determine whether
there is an equatorial continuity of the saccus, especially in grains viewed equatorially.
It is even possible that both bisaccate and monosaccate grains are produced in the same
species.

Failure to distinguish between taxonomic and morphologic characteristics may also
have contributed to the confusion. The infraturma Monosaccites Chitaley (Potonié and
Kremp) includes forms in which the 'reticulum of the sacci (*sic*) is mostly not abietinoid'

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EXPLANATION OF PLATE 77

Figs. 1–2. *Callandrium callistophytoides* Stidd and Hall. 1, Mature synangium in longitudinal section,
   × 25; slide 2296. 2, Three immature synangia in cross-section, × 36; slide 2271.

Figs. 3–13. Stages in development of *Vesicaspora*. 3–5. Successive focal levels of a decussate tetrad;
   slide 2256. 6, Distal view of grain with saccus beginning to protrude over sulcus; slide 2270. 7,
   Two microspores of a tetrad, lowermost with gaping sulcus (arrow); slide 2232. 8, Isobilateral
   tetrad (centre), bladder and sulcus apparent; slide 2238. 9, Two microspores of a tetrad (upper
   right), sulcus and bladder on each; slide 2232. 10–11, Two focal levels of a single microspore (centre
   left), sulcus with slight margo; slide 2262. 12–13, Somewhat older pollen, separated from tetrad,
   saccus enlarging; equatorial view of two focal levels, × 1000; slide 2261.

Fig. 14. Mature grain of *Vesicaspora*, equatorial view; cytoplasm-like object in body, × 1500; slide
   2292. All slides in University of Illinois Paleobotanical Collection, Morrill Hall, Urbana, Illinois.

(Potonié 1958). Because *Vesicaspora* has an abietinoid reticulum in the saccus, it is excluded from the Monosaccites, and placed in the Disaccites by Potonié (1958); he does note, however, that the 'sacci' are joined equatorially. In Potonié's scheme, it is not the number of sacci so much as the nature of the infrareticulum which places this monosaccate grain among others which are truly bisaccate.

Our interpretations of *Vesicaspora* can be better justified by our observations on saccus development.

Before doing this, however, we must clarify our concept of this genus. We are following the emendation of the genus by Wilson and Venkatachala (1963) based on *V. wilsonii*. Critical characteristics include an oval to circular saccus which envelops the central body in the equatorial region but not the cap and sulcus; saccus distally inclined; sulcus fusiform, extending across the central body at right angles to the long axis of the grain. These features can be seen in Plate 77, fig. 14, and Plate 78, figs. 1–7.

*Klausipollenites* Jansonius, which includes some species once assigned to *Vesicaspora*, lacks a clearly defined sulcus and does not have an equatorial connection between the sacci. Differences between *Falcisporites* and *Vesicaspora* may not be so easily identified; Clapham (1970) has noted intermediates between the two genera. For the most part, however, *Falcisporites* is bisaccate. But of these three genera, only *Vesicaspora* has been found in the Pennsylvanian, the others being Permian or younger.

## POLLEN DEVELOPMENT

All of our observations are based on cellulose acetate peel preparations of *Callandrium callistophytoides* and macerations of the mature pollen. Several stages in pollen development occur, and these can be most conveniently compared with developmental stages and the mature sculpture of living bladdered conifers.

In some of the young sporangia there is a rather disorganized mass of cellular material which may represent either the microspore mother cells or a very young stage in microspore development. The youngest preserved stage, however, is the tetrad of microspores, shown in Plate 77, figs. 3–5, 8, 10–11. In pine, Ferguson (1904) found a common microspore mother cell wall around young tetrads. According to Martens *et al.* (1967) this is composed of callose, a material not likely to preserve had it originally been present in *Vesicaspora*. Martens *et al.*, have also described the tetrad configurations in *Pinus sylvestris* L. Only tetragonal tetrads occur in this species, these being isobilateral, decussate, or intermediate. A decussate tetrad of *Vesicaspora* is shown in Plate 77, figs. 3–5; one can also be seen in Plate 77, figs. 10–11. An isobilateral tetrad is seen in Plate 77, fig. 8. Decussate tetrads predominate in *Vesicaspora*, perhaps 90% being of this type. Their orientation in sections of the sporangia is random, and in making peels some tetrads were undoubtedly cut (cf. Pl. 77, fig. 9). A gaping sulcus can be seen on the distal face in Plate 77, fig. 7, as well as figs. 10 and 11 in polar view. The sulcus at this stage seems to have a smooth, elevated margo, not apparent in all spores, nor in later developmental stages. In fig. 9, two spores of a tetrad are shown, with the obviously distal, wide sulcus in the left spore, and a narrower, long sulcus on the right one. The prominence of the sulcus is also seen in the spore in the upper left of the decussate tetrad in Plate 77, fig. 3.

The sculpture of the microspore is foveolate. This pattern can be seen in each of the spores in Plate 77, figs. 6–11, though the bladder is beginning to form in most of these.

Whether this is a pattern that occurs on the inside or the outside of the saccus cannot be determined, but the inference is that it is infra-foveolate.

Bladder development begins before separation of the tetrad (Pl. 77, figs. 3–5, 7–9). Separation of wall layers occurs uniformly around the equator of the spore (Pl. 77, figs. 10, 11) and from the flanks of the sulcus to the distal pole, though not over the region of the cap (Pl. 77, figs. 8, 9). We were able to see only two wall layers in these small spores, and believe that there is a separation between the ektexine and endexine at this stage. In living conifers, Pettitt (1966) has found two layers in the wall of *Pinus sylvestris* pollen. In late tetrad stage of *Vesicaspora*, before separation of the four spores, the saccus is a single unit; there are no protuberances in the distal region, flanking the furrow.

These spores are quite small. Based on measurements of 25 grains, their length, in equatorial view is 13·2–15·6 $\mu$m, and they are 6·6–8·8 $\mu$m along the polar axis. The bladder is only 1 $\mu$m wide at this stage.

Since tetrad separation occurs early, the illustrations of tetrads of mature spores by Wilson and Venkatachala (1963) and Millay and Eggert (1970) are probably of a fortuitous aggregation of four pollen grains in an apparent tetrahedral arrangement.

Separation of the saccus from the body continues after tetrad separation. In Plate 77, figs. 12, 13, two focal levels of a grain in equatorial view show expansion of the bladder, and the enlargement of the foveae in the lateral and distal regions. Plate 77, fig. 6, shows the enlargement of the saccus in distal view; the two inflated regions are apparent. The pollen wall is perceptibly but immeasurably thicker. It is still foveolate, but the foveae and intervening muri are slightly larger than they are in the tetrad stage. Spore size is no greater than before separation of the tetrad. Equatorial dimensions are 12–15 $\mu$m.

Plate 78, figs. 1–7, show a series of focal planes in polar view of a mature grain macerated from a sporangium. The cap region (fig. 1) is foveolate, comparable in structure to that of the entire grain while in the tetrad and shortly after bladder initiation. The margin of the inflated saccus is well defined in this region (fig. 2). No haptotypic markings occur. In this region, where saccus and cap join, the sculpture of the saccus is foveolate, becoming outwardly (marginally) progressively more coarsely infra-reticulate (fig. 2). The largest lumina of the infra-reticulum occur in the distal protuberances (figs. 6, 7). There is marked diminution of lumina size, to the infra-foveolate condition, where these protuberances flank the sulcus (fig. 7). Thus, the cap, which is not covered by the saccus, and the sulcus, where the saccus joins the body, have a comparable sculpture. The non-columellate nature of the muri of the infra-reticulum is apparent in figs. 6, 7. That the distal protuberances are small is shown in Plate 77, fig. 14.

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EXPLANATION OF PLATE 78

Figs. 1–7. Successive focal levels through a mature grain of *Vesicaspora*; slide 2272, Univ. Ill. Paleobot. Coll., Morrill Hall; ×1000. 1, Proximal surface (cap); outline of body seen as the darker circle peripheral to cap; a–a, line along which measurements of saccus length were made; b–b, same, for saccus width. 2–3, Cap, body and reticulation of saccus in lower foci. 4, Near optical section. 5. Just distal to optical section. 6–7, Near distal levels; sulcus, protuberances of saccus evident.

Fig. 8. Pollen grain of *Vesicaspora* with cytoplasm and nucleus-like objects in body; slide 2272, Univ. Ill. Paleobot. Coll., Morrill Hall; ×1000.

The body is nearly circular when seen in polar view and rounded-trapezoidal in lateral view. The saccus clearly has separated from the body except at cap and furrow region (Pl. 77, fig. 14; Pl. 78, figs. 1–7); the body is thus bounded by the endexine in non-polar regions as it is in modern conifers (Pettitt 1966).

In a number of mature grains, what appears to be cytoplasm, and perhaps even a nucleus (Pl. 78, fig. 8; Pl. 77, fig. 14) has been preserved.

Measurements of the mature pollen are as follows, in polar view: total length of saccus (a–a in Pl. 78, fig. 1), 39–48 $\mu$m; width of saccus (b–b in Pl. 78, fig. 1) 24–36 $\mu$m; body diameter 19–26 $\mu$m. There has been a three-fold increase in size from the tetrad to mature pollen.

## DISCUSSION

Our material of *Vesicaspora* is clearly monosaccate on the basis of the criteria we have chosen. The two distal protuberances which flank the sulcus are small; in polar view, the saccus is seen to be one continuous structure.

Because no modern cycadophyte possesses bladdered pollen (though cf. the illustration of *Encephalartos* pollen in Pettitt 1966) the only comparative material has been that of the bladdered conifers. Even so, remarkable parallels do exist. Tetrad configuration is like that of *Pinus sylvestris*, formation of the saccus parallels that of this and other species of pine, and shape of body is comparable.

One feature of saccus development, which does not seem to have been described previously, concerns the change in infra-sculpture of the saccus from the foveolate sculpture of the young grain to the reticulate sculpture of the mature saccus. Intermediate stages in development of the saccus suggest that there may have been a progressive increase in lumina size and murus height, that is the foveae enlarge to become lumina. In regions where there is no saccus, at the poles, the sculpture remains foveolate. The largest lumina occur where the saccus has inflated most, away from the body.

Although *Vesicaspora* is comparable in both development and mature form to the bladdered pollen of some conifers, we are undoubtedly dealing with an interesting case of parallel evolutionary development in two major groups of gymnosperms. It seems apparent that there is one major group of Palaeozoic and Mesozoic pteridosperms, represented by such genera as *Simplotheca*, *Callandrium*, *Pteruchus*, and *Caytonia*, which possessed bladdered pollen (Stidd and Hall 1970a). That this group is closely related to the true conifers is doubtful. Although this group has a time span which encompasses the appearance of earliest angiosperms, pollen morphology does not substantiate a relationship to them either. The second group, represented by *Medullosa* and exclusively Palaeozoic, had prepollen (*Schopfipollenites*). Ancestral to both these pollen types, Stidd and Hall (1970a) have suggested the pteridophytic pollen of the *Aneurophytales*.

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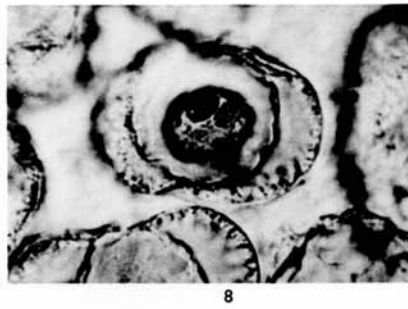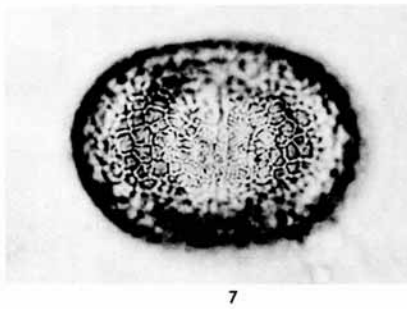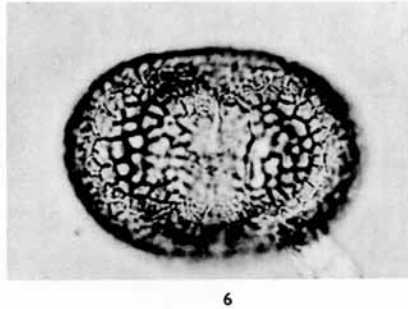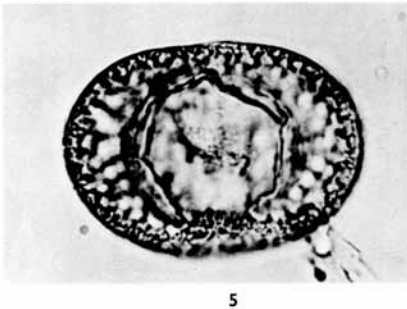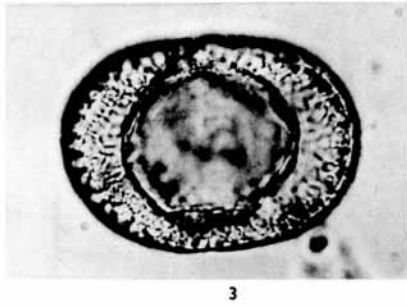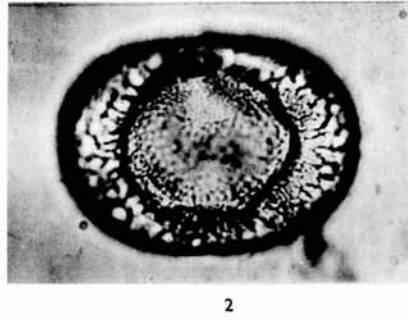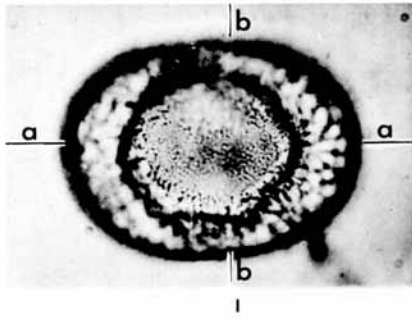
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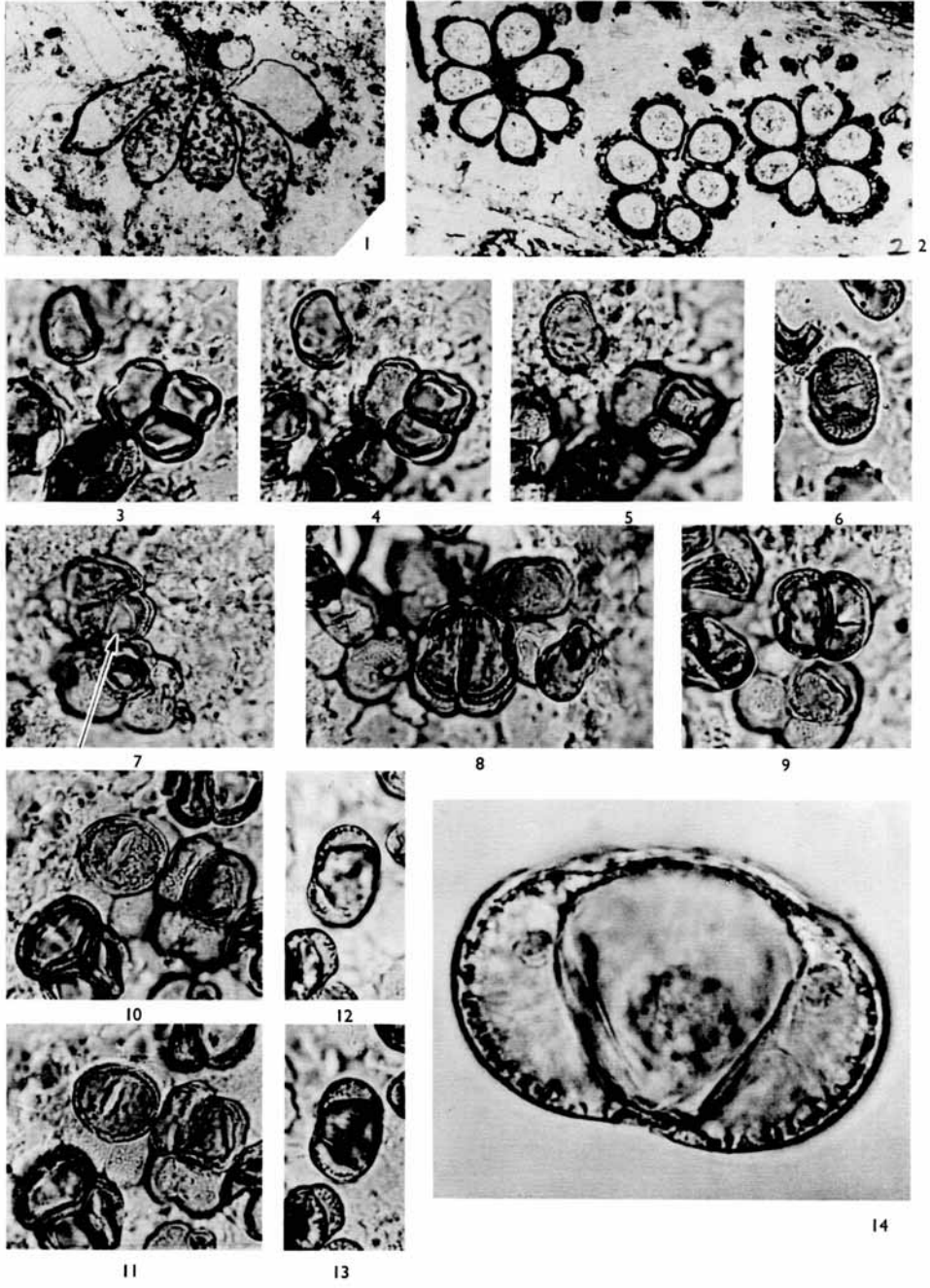
HALL and STIDD, Pennsylvanian pollen

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