

<sup>49</sup> Froier, K., Gelin, O., and Gustafsson, A., *Bot. Notiser*, **1941**, 199–216.

<sup>50</sup> Koller, P. C., *Proc. Roy. Soc. Edinburgh*, **B61**, 398–429 (1943).

<sup>51</sup> Canti, R. G., and Donaldson, M., *Proc. Roy. Soc. London*, **B100**, 413–419 (1926).

---

## THE SPORE DISCHARGE MECHANISM OF COMMON FERNS

BY ALLEN L. KING

DEPARTMENT OF PHYSICS, DARTMOUTH COLLEGE

Communicated June 6, 1944

Among ferns the Polypodiaceae are most common and are highly developed. In this family the mature sporangium, rather uniformly, is a flattened obovoid capsule supported on a long pedicel (*P*, Fig. 1). The unicellular thin side walls enclose the region in which spores develop. Along approximately two-thirds of the edge of this lenticular form, a single row of nearly cuboid cells (*A*, Fig. 1) become differentiated. This incomplete ring, the annulus, is prominent on the back and apex of the sporangium and is attached to the pedicel at the rear. From the annulus to the front of the pedicel a number of thin-walled cells complete the ring. Two of these cells meet in a straight line, the stomium (*S*, Fig. 1), and when the sporangium dehisces, cleavage first takes place along this juncture.

The annulus consists of thirteen or more cells with thickened inner and radial walls and thin flexible outer and side walls. The inner walls form a continuous band with crenations due to a slight arching inward at each cell. This band is very elastic and acts as a spring to expel the spores with considerable speed at the time of dehiscence.

When the sporangium becomes mature, evaporation of water from the annular cells induces sufficient stress to cause cleavage at the stomium. The line of cleavage follows cell boundaries toward the rear of the sporangium. Frequently weak lateral cells are split in two.<sup>1</sup> Meanwhile, the annulus slowly straightens and continues to evert sometimes to the extent that the two ends of the recurved annulus almost meet. Nearly all the spores are carried on the free end in a cup formed by the lateral walls of the sporangium. Suddenly the annulus snaps back to its original position and in the process it may catapult spores to distances of 1 to 2 cm.<sup>2</sup>

Although the function of the annulus in spore discharge was known prior to 1700, the details of the mechanism were not understood until the end of the last century. It was recognized that adhesion of the cell contents to the walls within annular cells is greater than cohesion. Careful observations revealed that the appearance of a bubble within the cell initiated the sudden snap of the annulus; and it was suspected that rup-

ture of the cell sap released the elastic energy of the bent annulus. In 1915 Renner<sup>3</sup> and Ursprung<sup>4</sup> independently measured the negative pressure required for bubble formation by two methods. They obtained values of 200 to 300 atmospheres.

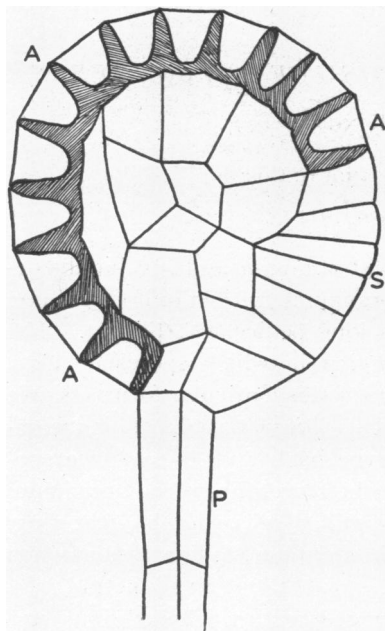


FIGURE 1

Side view of a sporangium showing location of the annulus *A*, the stalk or pedicel *P* and the stomium *S*. The hatched portions represent the thickened walls of the annular cells. Although spores usually may be seen through the transparent side walls of a mature sporangium, they have been omitted in this drawing.

be set up along *QR*. Each element of area  $l ds$  of the membrane is in equilibrium so that

$$T d\phi = q ds \quad (1)$$

Since  $T$  and  $q$  are constants, Equation (1) defines a circle of radius  $T/q$ . Thus the outer wall of the annular cell becomes a cylindrical surface of length  $l$  and radius  $T/q$ . Since the membrane is semicircular in cross-section at the instant of rupture, this radius equals  $m/\pi$  so that the tension  $T$  has the value  $qm/\pi$  and makes an angle  $\alpha = a/2r$  with the radial wall.

*Size of Sporangia.*—The annular cell consists of thick base and radial walls and thin flexible side and outer walls. During dehiscence the base becomes recurved, the radial walls remain relatively unchanged in shape although they become reoriented, and the weak side and outer walls are pulled in. For the following analysis the cross-section of an annular cell is assumed to have the form shown in figure 2. Since the outer wall of length  $m$  is observed to be almost flat, the initial pressure inside the cell probably differs from that outside by not more than a few atmospheres. The base of length  $a$  has a radius of curvature  $r'$  and the radial walls have a height  $b$ . Just before rupture the base becomes recurved until it has a radius  $r$ . Membrane  $m$ , which is relatively inextensible, takes on a semicylindrical form provided end effects are neglected. Width  $l$  of the cell is assumed to be unaltered by the process.

Suppose the difference in pressure across membrane *QR* is  $q$ , directed normal to the surface as shown in figure 3. A tension  $T$ , which is constant over the entire membrane, will

From figure 2,  $r'$  is found to be given by

$$m = 2(r' + b) \sin (a/2r') \tag{2}$$

and  $r$  by

$$m = \pi(r - b) \sin (a/2r). \tag{3}$$

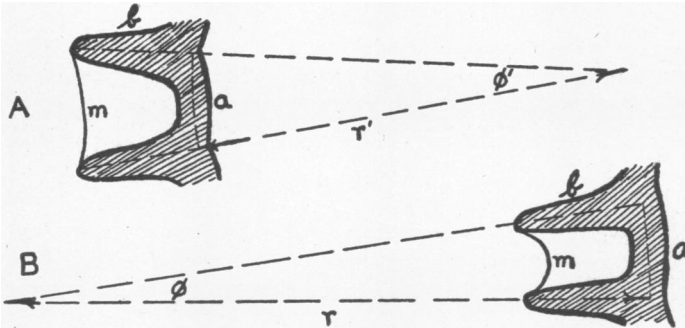


FIGURE 2

Cross-section of a single annular cell before dehiscence, *A*; at the moment of full eversion, *B*. *m* is a thin flexible membrane through which water is believed to pass during dehiscence.

The first terms in the expansions of the sine functions are sufficient for this analysis. On eliminating *m* from the resulting relations,

$$\frac{1}{r} = \frac{0.364}{b} - \frac{0.636}{r'}. \tag{4}$$

Values of  $r/b$ ,  $r'/b$  and  $r'/r$  are entered in table 1. The product  $rr'$  has a minimum value when  $r = 5.49b$  and  $r' = 3.49b$ .

TABLE 1  
RELATION BETWEEN INITIAL AND FINAL RADII OF SPORANGIUM

$r'/b$	$r/b$	$r'/r$	$r'/b$	$r/b$	$r'/r$
1.75	$\infty$	0.00	5.0	4.2	1.2
2.0	22.2	0.09	6.0	3.9	1.5
3.0	6.6	0.46	7.0	3.7	1.9
4.0	4.9	0.82	8.0	3.5	2.3

Since the outer wall becomes semicylindrical before bubble formation, the annulus must straighten out or recurve. The minimum value of  $r'/b$ , therefore, is 1.75 corresponding to  $r = \infty$ . If  $\theta'$  and  $\theta$  represent the initial and final angles subtended by *all* the annular cells, then

$$r'\theta' = r\theta. \tag{5}$$

The maximum value of  $\theta$  is  $2\pi$ , since the annulus can recurve only until its two ends meet. On the other hand,  $\theta'$  usually is not less than  $\pi$ . For these limiting values of  $\theta$  and  $\theta'$  the ratio  $r'/r = 2$ . In table 1 this ratio is seen to occur when  $r'/b$  is slightly greater than seven. Thus the radius of a ripe sporangium is not less than 1.75, nor greater than 7 times the height of an annular cell. As shown in table 2, average values of  $r'/b$  for seven species of ferns lie well within this range.

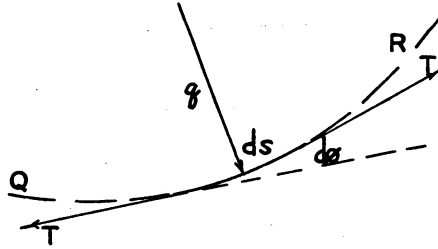


FIGURE 3

Cross-section of a portion of membrane  $m$  at the moment of full eversion showing element of length  $ds$ . The vector labeled  $q$  represents the force  $q l ds$  and the vectors labeled  $T$  represent the force  $T dl$ .

TABLE 2  
SIZES OF SPORES, SPORANGIA AND ANNULAR CELLS

SPECIES	$b$	$a/b$	$c/b$	$r'/b^*$	$l/b$	$e/b^\dagger$
<i>Cyrtomium falcatum</i>	30 $\mu$	0.63	0.27	3.5	2.0	1.3
<i>Dryopteris uliginosa</i>	31 $\mu$	0.74	0.26	2.6	2.1	1.1
<i>Phlebodium aureum</i>	44 $\mu$	0.69	0.18	3.8	1.8	1.0
<i>Pteris cretica</i>	38 $\mu$	0.59	0.22	3.8	1.5	1.4
<i>Pteris longifolia</i>	47 $\mu$	0.58	0.25	4.8	1.4	1.0
<i>Nephrolepis pectinata</i>	28 $\mu$	0.68	0.29	4.0	1.6	0.9
<i>Nephrolepis exaltata</i>	29 $\mu$	0.76	0.25	2.6	2.0	1.0
Averages	35 $\mu$	0.67	0.25	3.6	1.8	1.1

\* Usually sporangia have elliptical cross-sections. Major and minor axes were measured and  $r'$  was computed for the middle of the annulus.

† Frequently, spores are slightly ellipsoidal. Only the non-fertile spores of *Nephrolepis exaltata* (Boston fern) showed considerable variation in size.

*Young's Modulus of the Annulus.*—Consider a single annular cell  $OPQR$  of a fully everted sporangium, as shown in figure 4. Membrane  $QR$  is a cylinder of radius  $T/q$ , as shown above, where  $q$  is the negative pressure of the cell sap on the membrane (the pressure outside is negligible).  $q$  acts uniformly over the entire inner surface of the cell. For the membrane  $QR$ , however, it may be replaced by the tension  $T$  acting along the tangent to the membrane at the juncture with the radial walls.

The moment of the forces on cell surfaces  $OPQ$  about  $O$  consists of the moment of  $T$ , the moment of  $q$  over surfaces  $OP$  and  $PQ$  and the bending moment of the elastic forces in the base  $OP$ . The effect of the weight of cells attached to  $PQ$  is very small compared with the other stresses and may be neglected. To the approximations involved here the bending moment of the base equals  $EI(r + r')/rr'$ , where  $E$  is Young's modulus of the base material,  $I$  is the moment of area for a transverse section of the base and  $r$  and  $r'$  are the radii of curvature before and at the instant of full eversion. The annulus is assumed to be in equilibrium just before rupture occurs, so that

$$EI(r + r')/rr' = ql\{\frac{1}{2}b^2 + r(r - b)(1 - \cos \phi)\} + Tl\{r \sin(\alpha - \phi) - (r - b) \sin \alpha\}. \quad (6)$$

If the transverse section of the cell base has height  $c$ , the moment of area  $I$  about the central line is  $lc^3/12$ . With this value of  $I$  and for small angles, equation (6) reduces to

$$E = 6qb^2rr'/c^3(r + r'). \quad (7)$$

With  $c = b/4$ ,  $r = 5.5b$ ,  $r' = 3.5b$ , and  $q = 200$  atmospheres, Young's modulus for the annulus comes out approximately  $1.6 \times 10^{11}$  dynes/cm.<sup>2</sup> This value is about 25 per cent greater than that reported by Press<sup>5</sup> for viscose rayon yarn. Common green woods<sup>6</sup> have moduli ranging from 1.0 to  $1.5 \times 10^{11}$  dynes/cm.<sup>2</sup> Since the thickened wall of the annular cell is especially spring-like, its modulus of elasticity should be somewhat greater than that for common wood fibers. The ratio of Young's modulus to the density of the annular walls is greater than the same ratio for many other solids.

*Initial Speed and Range of Spores.*—Since the thickened base of the annulus is a continuous structure, it may be considered a circular arc fastened to the pedicel at one end. When the sporangium is fully everted sixty odd spores are held within a cup formed by the lateral walls which remain fixed to the free end of the annulus. The total potential energy of the everted annulus is

$$W = \frac{1}{2}naEI(1/r + 1/r')^2, \quad (8)$$

where  $n$  represents the number of cells in the annulus and the other symbols have already been defined.

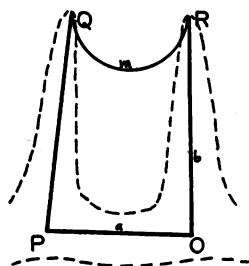


FIGURE 4

Cross-section of a single annular cell at full eversion. For the analysis in this paper the cell is assumed to have the form  $OPQR$ . The dotted lines indicate the actual outline of the cell walls.

When the vapor bubble forms, the negative pressure is assumed to be entirely released; so that the annulus springs back with a snap to its original position. It is further assumed that the cup with spores is fastened to the end cell of the annulus. Even if the cup is three or four cells from the end, the initial speed and range of the spores are increased by less than 100 per cent. As the cup slips from behind it, the spore mass acquires momentum directed away from the sporangium. To a first approximation, the radius of the annular arc at the moment the spores leave is

$$R = rn/(n - 1). \quad (9)$$

This relation arises if the angle subtended by the annular arc from pedicel to spore mass, initially  $(n - 1)a/r$  and finally  $na/R$ , is supposed to remain unchanged during the discharge process. The decrease in potential energy experienced by the annulus as the radius changes from  $r$  to  $R$  is

$$V = (aEI/r^2)(1 + r/r' - 1/2n). \quad (10)$$

In order to obtain an upper limit for the average speed  $v$  of spore ejection, this change in potential energy is assumed to be transformed entirely into kinetic energy of the spore mass. The kinetic energy of the moving annulus and cup and all energy losses are neglected. The kinetic energy gained by 60 spores is

$$U = 5\pi\rho e^3v^2, \quad (11)$$

where  $\rho$  is the density and  $e$  is the diameter of each spore.

Equate  $U$  and  $V$ , eliminate  $EI$ , and solve for  $v$ . Because  $r'/2n(r + r')$  is much less than unity, the average speed comes out

$$v = (aqb^2/10\pi\rho e^3r)^{1/2}. \quad (12)$$

On substituting average values of  $a$ ,  $b$  and  $e$  from table 2,  $r = 5.5b$ ,  $\rho = 1$  g./cc. and  $q = 200$  atmospheres, the speed of ejection of the spores is calculated to be 10 meters/sec.

By application of Stoke's law, the distance a spore may travel is given by

$$d = ve^2(\rho - \rho')/18\eta, \quad (13)$$

where  $v$  is the initial speed,  $e$  is the diameter and  $\rho$  the density of the spore, and  $\eta$  is the viscosity and  $\rho'$  the density of air.<sup>7</sup>  $\eta = 0.00018$  poise at 20°C.,  $\rho = 1$  g./cc., and  $\rho'$  may be assumed negligible. Using these data and the average value of  $e$  from table 2 (nearly 40 microns) in equation (13), the range of spores is computed to be approximately 5 cm. Although this result is more than twice the observed values, the discrepancy is not unexpected. Energy losses were neglected, the mass of the spore cup was not taken into account and the problem was otherwise much idealized.

If the negative pressure  $q$  were less than 10 atmospheres or greater than

10,000 atmospheres, Young's modulus of the annular arc and the range of spores would have come out too small or too large. A sporangium can evert again and again by alternate imbibition of water and desiccation after the spores have been expelled, even in the case of herbarium specimens more than fifteen years old.<sup>8</sup> This suggests that the annular cells of a spore-filled mature sporangium contain water and that this water is ruptured at the time of bubble formation. *The above computations, therefore, yield additional evidence for the belief that the tensile strength of water is around 200 atmospheres.* Haller<sup>9</sup> obtained 200–300 atmospheres by means of a piezo-electric device in a stream of water where cavitation occurred. Measurements by Dixon<sup>10</sup> and by Vincent<sup>11</sup> using Berthelot's method gave values as high as 150–200 atmospheres. Many experimental and theoretical values are in marked disagreement with these results; but an extensive discussion and evaluation of them is beyond the scope of this paper.

The author here expresses his appreciation for the use of the greenhouse and the helpful advice given by Professor Charles J. Lyon of the botany department at Dartmouth College. Also he is much indebted to Drs. L. J. Briggs and L. B. Tuckerman of the National Bureau of Standards for pointing out two errors in the original manuscript.

<sup>1</sup> Atkinson, G. F., *The Study of the Biology of Ferns by the Collodion Method*, Macmillan and Co., New York (1894), p. 68.

<sup>2</sup> Ingold, C. T., *Spore Discharge in Land Plants*, Oxford University Press, London (1939), p. 119.

<sup>3</sup> Renner, O., *Jahr. f. Wiss. Botanik*, **56**, 647 (1915).

<sup>4</sup> Ursprung, A., *Ber. d. Deutsche Bot. Gesell.*, **33**, 153 (1915).

<sup>5</sup> Press, J. J., *Jour. App. Phys.*, **14**, 224 (1943).

<sup>6</sup> *International Critical Tables*, Vol. II (1927), p. 6.

<sup>7</sup> Buller, A. H. R., *Researches on Fungi*, Vol. 1, Longmans, Green, and Co. (1909), p. 190.

<sup>8</sup> Atkinson, G. F., *op. cit.*, p. 71.

<sup>9</sup> Haller, P. de, *Schweizerische Bauzeitung*, **101**, 260 (1933).

<sup>10</sup> Dixon, H. H., *Transpiration and the Ascent of Sap in Plants*, Macmillan and Co., London (1914).

<sup>11</sup> Vincent, R. S., *Phys. Soc. Proc.*, **53**, 126 (1941); Vincent, R. S., and Simmonds, G. H., *Phys. Soc. Proc.*, **55**, 376 (1943).