WILLIAMSONIELLA LIGNIERI: ITS POLLEN AND THE COMPRESSION OF SPHERICAL POLLEN GRAINS

by TOM M. HARRIS

ABSTRACT. The type specimen of the Bennettitalean flower *Williamsoniella lignieri* (Nathorst) on reinvestigation proved to have an intact pollen sac yielding well-preserved pollen. The pollen grains resemble *Exesipollenites scabratus*. Most of the grains are distorted by crushing and the distortion of outline is related to folds on the surface. Hollow balls made of various materials were compressed between flat surfaces and their various secondary distortions are described; one kind of ball mimicked the forms seen in *W. lignieri* pollen and other balls with different mechanical properties mimicked the distortions of miospores of other plants. When compressed in a matrix (whether itself compressible or not) the hollow balls distorted differently. There is scope for further experimental study of compression in a matrix.

THE specimen described here was collected by A. G. Nathorst in 1909 from the classic Lower Estuarine Plant Bed (Lower Bajocian) of Whitby, Yorkshire. Nathorst described it in 1909 as a problematic male flower but the specimen, which is preserved in the Section for Palaeobotany of the Riksmuseum, Stockholm, has remained obscure. I re-examined it at Stockholm in 1972 and realized that it is probably the same species as *Williamsoniella papillosa*, also from Whitby and described by Cridland in 1957.

WILLIAMSONIELLA LIGNIERI (NATHORST, 1909)

1909 *Williamsonia*(?) *Lignieri* Nathorst, p. 20, pl. 4.
1915 *Williamsoniella Lignieri* (Nathorst), Thomas, p. 154. (Name, discussion.)
1933 *Williamsoniella Lignieri* (Nathorst), Florin, p. 11, text-figs. 3B, 5B (stomata).
1957 *Williamsoniella papillosa* Cridland, p. 383, text-figs. 1–3 (various organs). Mention of *W. lignieri* on p. 388.
1967 *Williamsonia lignieri* Nath., Potonié, p. 122, pl. 13, fig. 258 (pollen).
1969 *Williamsoniella lignieri* (Nathorst), Harris, pp. 142, 144. (Cited as possibly the same as *W. coronata*.)
1971 *Williamsoniella papillosa* Cridland, Konijnenburg van Cittert, p. 35, pl. 7, fig. 5 (pollen).

General discussion. The specimen is the base of a flower compressed to form a disc of coal about 0·5 mm thick. The coaly substance consists of several layers of plant material but the matrix between them is so thin that they cannot be separated with needles though the cuticles separate on maceration. Some of the coal is missing, no doubt having been used by Nathorst and probably by Thomas for cuticle preparations, so part and counterpart do not correspond fully. The original drawings of the part and counterpart are reproduced here (Pl. 15, figs. 2–3) together with new photographs (Pl. 15, figs. 5–6). The part is a view from below morphologically (text-fig. 1B) and most of it shows lanceolate scales but on one side (Pl. 15, figs. 2, 3, 6) it shows fine radiating ridges. These radiating ridges are the stalks of interseminal scales in an approximate transverse section of the gynaeceum near its base. Nathorst called them

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the disc or collar, terms he used for the corresponding part of *Williamsonia* flowers. All the upper interseminal scales and seeds were lost before preservation.

The specimen had not been prepared by picking away rock matrix and its margins were still buried. When cleared, a few crumbs of coal came away and were macerated with useful results. The separate bract shown on the left of Pl. 15, figs. 3, 6 (which Nathorst recognized as belonging to *W. lignieri*) also came away and also a small piece of coal just at the edge of the radiating lanceolate scales (seen at 2 o'clock in Pl. 15, figs. 3, 6, and marked with an arrow). This proved to be a pollen sac. It had been drawn by Nathorst's artist but had not been described. The original drawings are excellent but do not look quite like the photographs. They show individual bracts more clearly; no doubt varied lighting was used to show their margins. They also leave things out, for instance the imprint of the free bract is omitted from Pl. 15, fig. 2 but seen in fig. 5. The rock is trimmed down artistically in both drawings but in fact both sides are fair-sized blocks which show various associated leaves.

Nathorst (1909) and Thomas (1915) differed in their interpretations of the parts of the flower and sometimes I follow the one, sometimes the other. For Nathorst (1909) the radiating scales were ordinary floral bracts, the organs which when separate are called *Cycadolepis*, and this is here accepted fully. But he does not relate his cuticle preparations (his pl. 4, figs. 9, 10) to the two surfaces of one of these bracts. He found some unusual looking interseminal scale heads with adherent pollen, and misinterpreted them as microsporangia. Thomas on the other hand recognized the interseminal scales but interpreted the floral bracts as microsporophylls. Both recognized the floral axis in the middle. This forms a rod of coal passing obliquely into the rock. No doubt compression of the matrix has greatly exaggerated the obliquity of this axis (text-fig. 1).

It was the perianth bracts that first indicated that *W. lignieri* and *W. papillosa* were the same. They have marked specific peculiarities. They are unusually small, only about 11 mm long, a dull black, not shining like many kinds of *Cycadolepis*. As usual they are covered with wrinkles, these being longitudinal in the middle region but divergent near the sides. The wrinkles are exceptionally fine, only 0·5 mm from crest to crest in the middle region, but further apart near the edges. I believe that these wrinkles were produced in preservation following the decay of the inner tissues (and I have simulated them in the scales of the artichoke *Cynara*) but none the less they are

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EXPLANATION OF PLATE 15

Figs. 1–3, 5–9. *Williamsoniella lignieri* Nathorst. 1, Pollen grain showing the pore with a clear margin, × 1500. 2–3, Copies of original figures of *W. lignieri* from Nathorst 1909, pl. 4, fig. 2, 1. Fig. 3 shows the separate bract and at 2 o'clock the pollen sac now marked with an arrow. 5–6, Photos of Nathorst's Holotype. Fig. 6 (as fig. 3) shows the pollen sac, marked with an arrow. These are bits of two associated *Nilssoniopteris major* leaves below the flower. Photos by Mr. H. Samuelsson, × 2. 7, 8, A pollen grain at two levels of focus. Fig. 7 shows the pore as a vague pale area; there is corrosion or extraneous matter on the left. In fig. 8 the margin of the pore is partly in focus. × 1500. 9, A pollen grain with a pale area but no definite pore margin is visible, × 1500.

Figs. 4, 10–14. Experimental compression of table tennis ball. 4–10, Upper and under sides of a table tennis ball compressed in dry cotton wool matrix after weakening the equator with six small cuts (p. 147). 11–12. Upper and under sides of table tennis ball compressed in dry cotton wool (p. 146), illuminated from top right. 13, 14. Upper and under sides of table tennis ball compressed in sawdust (p. 145).

PLATE 15


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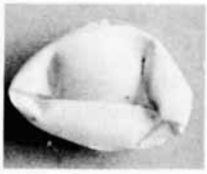
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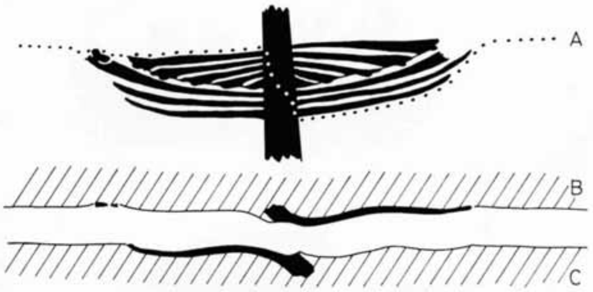
HARRIS, *Williamsoniella*



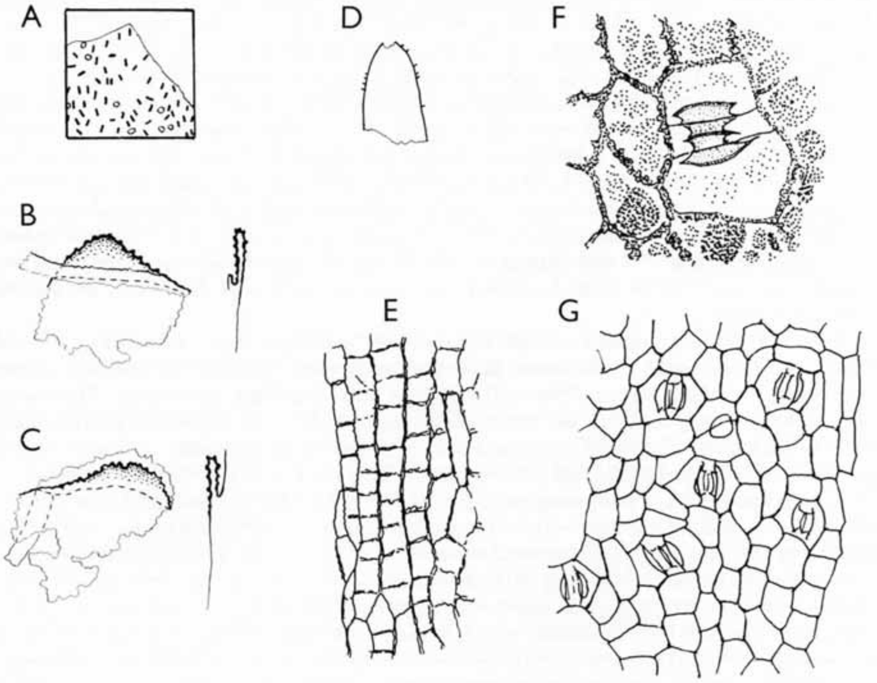
TEXT-FIG. 1. Imaginary longitudinal sections of holotype specimen. A, flower base as buried in mud but uncompressed. On the left a microsporophyll has one pollen sac but the rest is missing; the microsporophyll on the right has lost its pollen sacs. The dotted line is the future plane of rock splitting. The specimen is slightly tilted, the axis being not quite vertical. B, C, part and counterpart after compression which has made the axis seem more oblique but lateral organs almost horizontal. Magnification about 2·5.

characteristic of the species. Minute hairs, 0·5 mm long occur thickly on the edges of the free bract but not on its surface. They are not to be seen satisfactorily at the edges of bracts of the flower but cuticle preparations show that they were present there also.

Although the bracts have thick cuticles, originally 4–8 μm (estimated from folds), they are broken by cracks and the preparations are all small bits, but they do include margins where the two surfaces, stomatal and non-stomatal, join. The stomatal side is assumed for description to have faced downwards (or outwards) as it certainly does in some other Bennettitalean flowers. The upper (adaxial) side is of constant structure but the lower has very varied numbers of stomata; perhaps (on analogy with artichoke scales) those with few are inner scales with little photosynthetic tissue. The two surfaces are figured here (text-fig. 2) at a higher magnification than in Nathorst's photographs. Two peculiar features are emphasized; most of the stomata have apertures parallel with the long axis of the scale and the subsidiary cells are large and look pale. Bracts with numerous stomata show about 100 per sq. mm. which is exceptional for a *Cycadolepis*, but others have very few. The free bract has but few and these are near the apex. Hair bases are rare on the surface but an occasional ring-shaped print on a cell may represent a hair base. On the margin the hairs may be so crowded as to be in contact. They have very delicate cuticles and as far as is known are unicellular.

Nathorst's figures of adherent pollen show round or elongated grains about 25 μm wide, mostly with one or two parallel folds but one with crossed folds and one round one unfolded. Potonié (1967) examined Nathorst's slides (which had deteriorated through desiccation) and figured a rounded grain about 30 μm wide with a single mark regarded as a colpus. He remarks that most grains are spindle shaped. We only know the microsporophyll of Nathorst's specimen from the pollen sac just beyond the bracts. This is at about 12 mm from the flower centre but from Cridland we know that the microsporophyll was over 20 mm long, so this at 12 mm should be one of the lower pair. Everything beyond it is missing. There may well be a complete ring of microsporophyll bases concealed between the robust bracts and robust interseminal scales, but the microsporphylls are delicate and with delicate cuticles which would escape recognition in cuticle preparation unless deliberately searched for and even then might be missed.

This pollen sac or synangium was recognized as one only after maceration. It gave a compound block of tissue nearly 2 mm × 0·4 mm and this on further maceration gave some unit blocks of pollen about 0·4 mm × 0·1 mm which are taken to be the contents of single sporangia and the best of these on still further maceration broke up to give individual pollen grains. The macerations were carried out very gently with diluted acid in the hope of saving possible delicate tissues and even after the third treatment the pollen mass was only partly disintegrated. Beside the pollen there were delicate and uninformative cuticles of about three kinds. The pollen grains agree in size and some other features with the few seen in Nathorst's slides.



TEXT-FIG. 2. A, distribution orientation of stomata on bract cuticles. The base is 1 mm. Circles are possible hair bases. B, C, two interseminal scale heads in oblique compression, features at a lower level shown by broken lines. At the right of each is an imaginary section from top to bottom, both × 50. D, apex of a bract showing a few marginal hairs, × 12·5. E, adaxial cuticle of bract, × 200. F, stoma of bract, it is unusual in being transverse but otherwise normal. Surface thickenings stippled, × 400. G, abaxial cuticle of bract, stomatal apertures longitudinal. There is a ring on a divided cell which may be a hair base, × 200. All preparations from type specimen in Stockholm.

The coal from the edge of the specimen gave some interseminal scale head cuticles. They are compressed obliquely, as though they were situated half-way from the lower pole to the equator of the gynaeceum, while Nathorst's preparations, which were evidently from the base of the gynaeceum, are so placed that the head is pressed out flat. The new ones are useful because they are more like the scale heads prepared by Cridland from near the top of his '*W. papillosa*' gynaeceum than are those of Nathorst. In particular they are small, have a strongly raised central boss where the cuticle is thick, but it quickly becomes delicate towards the margins. Most of Nathorst's scale heads were almost flat and their cuticles were evenly thick to their edges, but there the cuticle bends inwards and becomes delicate abruptly and adheres to the edge of the next scale. No ovules are seen in any preparations of the holotype and they are not to be expected at the base of a gynaeceum.

Identification of Williamsoniella papillosa *with* W. lignieri. The specimens, although from the same locality, look different. *W. lignieri* is a nearly intact flower base compressed vertically but Cridland's specimens are fully disintegrated. The floral axis, the bracts, and the microsporophylls were separate but found on the same blocks. Just a few interseminal scales and ovules (perhaps abortive ones) remained at the top of the floral receptacle and most of the pollen sacs were empty but one had a few pollen grains sticking to a lining membrane. Cridland (1957) mentioned the bracts but did not describe them. The bracts on Cridland's blocks are small, 10 mm–15 mm long, dull black, have the same fine wrinkles and minute marginal hairs and above all have similar well-characterized cuticles. As in *W. lignieri* some have many stomata but some very few. As mentioned the interseminal scale heads now prepared are similar to some of those in Cridland's preparations (though less like the one he selected to figure).

At first the pollen seemed to differ but it is now found to agree. The grains Cridland selected and figured at × 900 (under my supervision) were broadly oval and each shows a strongly marked groove. The wall was thin and described as smooth. They were 27 μm long which is within the range of *W. lignieri*. Then Konijnenburg van Cittert (1971) examined Cridland's preparation and gave photographs of some pollen grains at × 1500 and a detailed description of the wall. She recognized a fine sculpture of a network of ridges enclosing pits about 1 μm wide. She was doubtful whether the groove in Cridland's grains was a true colpus. Neither author mentions a pore but it may be this was seen but dismissed as an effect of corrosion. The preparation shows only about thirty grains sticking to the pollen sac cuticles and half of these are obscure. With so few pollen grains and these only moderately clear a good deal of selection is necessary and it is hard to decide which features are original and which are effects of corrosion or distortion. On re-examination of Cridland's slide in the British Museum, a pore-like pale area was noted in sixteen of the grains (such an area is seen also in Konijnenburg van Cittert's pl. 7, fig. 5 top left and middle left grains but it is not indisputably a pore).

The different form of Nathorst's specimen and those of Cridland call for comment and a possible explanation. Cridland's seem in the natural state for a fructification that has fulfilled its function; it is Nathorst's partly intact one, still with unliberated pollen that is surprising. I suggest that it may be a slightly immature flower which had been attacked by an animal that had devoured the main part of the gynaecium and all but one of the pollen sacs but had left the tough bracts and gynaecium base.

Attribution to a leaf species. A main aim of my work has been to relate fossil reproductive organs to the far more abundant leaves and for this association in the field gives valuable indications, at least as probabilities. Cridland's material of *Williamsoniella papillosa* from Whitby is strikingly associated with the leaf *Nilssoniopteris major* (which is nowhere as abundant as at Whitby). We have long suspected or believed that *Williamsoniella coronata* belonged to *Nilssoniopteris vittata* so it was natural to look for a similar leaf for *W. papillosa*. But the association of *W. lignieri* with *N. major* was just as close; the block with the holotype has five fragments of that leaf but nothing else to which the flower is likely to belong. So the two flowers seemed for a short time to be rival claimants for a single kind of leaf but with their synonymy rivalry disappears.

THE POLLEN OF *WILLIAMSONIELLA LIGNIERI*

Description. Pollen grains almost circular and mostly about 25 μm in diameter (originally nearly spherical). Wall without any ridges or furrow (colpus) but with a single round or oval pore, edge of pore neither raised nor thickened, size typically 6 μm × 8–10 μm but sometimes larger, up to 15 μm × 12 μm in a large grain, edge of pore sometimes distinct but often ill marked. Pollen grain wall thin, up to 1 μm thick but often less, when well developed showing a fine network of ridges enclosing pits. Konijnenburg van Cittert (1971) gives in addition (for *Williamsoniella papillosa*) wall (exine) 0·5–1·0 μ thick; nexine smooth, very thin; sexine with columellae—and capita—layer; columellae very short, indistinct, capita spherical, laterally fused, forming a reticulum; lumina of reticulum wider than muri; muri about 0·5 μ wide, lumina 1 μ". I do not doubt these additional details but while I sometimes thought I perceived them, I could not do so consistently. But the reticulum on one of the thicker walled grains is illustrated in text-fig. 3C.

Discussion. Fortunately the grains all appear to belong to the one species without a single contaminant spore. They are as usual fully flattened, the upper and lower walls pressed together and many are obviously distorted and show compression folds of various kinds. They are neither pitted with pyrite crystals nor corroded in the manner that is attributed to bacteria. Nor have they indentations attributable to mineral crystals in the matrix. One grain showing possible corrosion is shown in Pl. 15, fig. 7, but the effect may be due to extraneous matter. But although there are many clearly visible grains, the population as a whole remained rather under-macerated after its three mild treatments and a great many grains are still in compact masses and only dimly visible. There are a very few grains, less than 1%, with irregularities in their outline that I cannot attribute to vertical compression but dismiss as having first been compressed in other planes. The pore may be seen anywhere in the middle, half-way out, or at the edge and equally in round or elongated grains; also the pore has no obvious relation to folds. For instance it might be in the groove between two folds or on the back of the grain opposite the groove. These observations seemed consistent with the idea that the original shape was nearly spherical, without any predetermined groove or folds.

This conclusion was arrived at only after the pollen grains had been measured a considerable number of times and recorded in increasing detail. At first merely the mean length and breadth, the total range and standard deviation were recorded, but then it seemed worth dividing them into three groups, the roundest (two axes equal within 3 μm), the longest (two axes differing by 10 μm or more), and the middle group, and giving means, ranges, and standard deviations. At the same time the kinds of folds were recorded and a relation became obvious. This led to still another survey when the grains were divided as much as possible on their shape into classes with axes differing by 0, 1, 2 up to 17 μm. At the same time the folds were recorded in six classes—(*a*) no visible folds; (*b*) a minute concentric one at the very edge (making a double edge); (*c*) strong folds of nearly concentric course forming a wreath half-way between the centre and the edge; (*d*) crossed folds, one on the top wall, one beneath; (*e*) a longitudinal groove flanked by two folds, and finally (*f*) a single strong longitudinal fold. Certain kinds of folds seen in spores of various other plants (for instance many small wrinkles) were never met. Two grains out of two hundred were rejected as shrivelled but many still in compact masses were too obscure to measure.

This analysis was successful in indicating that all folds are secondary but it is not certain that the original shape was a perfect sphere; it might have had one axis perhaps 2 μm longer than another. It is also possible that compression might have produced a slight general change in diameter. A main fact that emerged is that the rounder a grain the smaller is its longest diameter. The perfectly round grains were not only the smallest (mean 24·5 μm) but also the least varied in size and range recorded 22–29 μm, standard deviation 1·5 μm. As one takes progressively more elongated grains the mean maximum diameter increases, the mean minimum decreases and the variability of both, as well as the recorded range, increases. For the group of grains where the axes differ by 3 μm the long axis is mean 25 μm, range 21–31 μm. For the group where the axes differ by 10 μm the mean of the long axis is 33 μm, its range 26–38 μm and the standard deviation 5 μm. These figures may not be very significant but they show a trend. The short axis of this last group had a mean of 19 μm, range 13–24 μm, and standard deviation of 3 μm. The numbers of grains of each diameter in a count are given in a histogram in fig. 4 but the six classes of folds are reduced to two. Folds of the kinds *a*, *b*, *c*, *d* which are thought not to alter the outline of the grain much are taken together and the single longitudinal groove with one or two folds, *e*, *f* are taken together. The pollen grains in Cridland's preparation of *Williamsoniella papillosa* show a similar range of distortions of outline and surface folds.

The pore of *W. lignieri* is the most unexpected feature of its pollen grain for nothing like it had been recorded for the Bennettitales. It was, however, likely it would be seen in some fructification since the dispersed pollen resembling *W. lignieri* pollen, *Exesipollenites* Balme, or *Spheripollenites* Couper is widespread and often abundant in Yorkshire plant beds. Even in grains with the clearest pores it is difficult to decide whether the pore is open or had a very thin membrane.

The pollen of *Williamsoniella coronata*, described in detail by Konijnenburg van Cittert (1971) agrees in its size and unusually broad shape and its thin wall, described as thinner than in most grains of *W. lignieri*. She could detect no sculpture on the wall, but neither can I on the thinner walled *W. lignieri* grains. She described it as colpate, as previous authors had all done, but again over half the grains of *W. papillosa* have folds which could be taken for a colpus. No one has reported a pore in its wall, but I note on one of her figures (pl. 7, fig. 4) a pale spot which could be a pore. Plainly this pollen needs fresh study. There is a real difference in shape between the pollen grains of both these *Williamsoniella* species and those of all other Bennettitales I have seen under the microscope or as photographs. All the others are elongated and mostly a good deal larger. Some grains of *W. papillosa* may indeed be just as narrow but the whole population shows that these are distorted. No doubt too the colpus of the normal Bennettitalean grain is real but the colpus-like folds of distorted *Williamsoniella* grains raise slight doubts. There is a case for the experimental compression of plastic ellipsoidal balls.

No other gymnosperm with similar pollen has been described. The dispersed grains *Exesipollenites scabratus* which look similar have been tentatively referred to the conifers mainly because some Taxodiaceae have a single 'pore', but it is different, being the end of a conical papilla. It therefore is seen in surface view as a pore with a thickened rim. *E. scabratus* which has been figured by Couper 1958 from Yorkshire and by Tralau 1968 from the Middle Jurassic of Scania is similar in size and shape but the wall is thicker and more distinctly marked. It may be that the better characterized grains have been selected for figures but it is also possible that the name covers a number of species differing slightly in these respects.

THE COMPRESSION OF VARIOUS SPHERICAL MODELS IN RELATION TO *WILLIAMSONIELLA LIGNIERI* AND OTHER FOSSIL POLLEN

This section deals with distortions arising when spores are compressed between surfaces—the pollen sac walls for *W. lignieri* and boards or glass plates for the models. Although there are references to similar features to be seen among spores dispersed in rock matrix, the conditions of compression differ considerably and, while I believe many of the distortions apply to dispersed spores, others do not or only do exceptionally. My conclusions must not be applied indiscriminately to dispersed spores.

I had previously thought very little about the compression of spores except to regard the secondary distortions as a nuisance, to be recognized as distortions and so to be avoided as pitfalls and to be eliminated from descriptions. I had never welcomed them as useful evidence as I try to do here. Nor can I find any papers that do anything near this except for Potonié 1962 who analyses and classifies the folds on fossil spores of many original forms. He convinced himself that the folds are by no means casual but were related to the original form in an orderly way. They were therefore to be considered as features worthy of record. But I can find no record of any experiment to produce folds in models. Here I deal only with spheres, the simplest form, and as it happens the form of *W. lignieri*.

In their survey of the form of *Cicatricosisporites* Hughes and Moody-Stuart (1969, pp. 103–106) regarded many of the unusual forms as distortions caused in preservation. The physical distortions of compression and inflation and the chemical ones of various kinds of corrosion cause striking changes in the wall sculpture. The major distortions of these miospores are, however, different from those of *W. lignieri* for while bursting is common in their spores, gross folding of the wall is not. No burst grains were seen in the sample of *W. lignieri* but bursting is often seen in Bennettitalean pollen (Nathorst 1911). In Recent plants, bursting often happens when healthy pollen falls into fresh water. Clayton (1972) describes a remarkable deformation of the miospores of *Dictyotriletes admirabilis*, which when compressed in a sporangial mass take strong imprints from other spores lying immediately above them but in other respects their distortions are slight. While this distortion has no similarity to those dealt with here, it is relevant in that it reveals a mechanical property of the wall.

The simple, qualitative experiments described below are only justifiable in so far as they give ideas which seem useful when applied to real fossils. They can suggest good ideas and they can discredit bad ones. For me they did both.

In *W. lignieri* the pollen is not in a matrix of mud but in the sporangium wall, itself part of a pollen sac. I imagine that before it was compressed the whole fossil had been buried in mud and the more labile materials had decayed. The pollen grains would be mere bags of water floating in the water-filled sporangium and the water both in the grain and in the sporangium, as well as in the surrounding mud, would drain away as compression occurred. And when compression did begin it would be between the firm walls of the sporangium and therefore somewhat similar to my experiments with hollow balls compressed in air between hard surfaces.

For my experiments I used various hollow spheres made of different materials. The most useful was a particular plastic ball sold under the name 'playball' and I shall refer to it by that name. This 'playball' when punctured to let out air had a skin which when compressed mimicked astonishingly closely the various forms of compressed *W. lignieri* pollen. Other balls were constructed out of materials selected for their peculiar properties in the hope that they might throw light on the mechanics of the deformation of a sphere. The more successful experiments of this series are mentioned below. A good many of the effects produced, though not like ones seen in *W. lignieri*, did mimic distortions of other dispersed miospores.

The specially constructed balls were made as follows. First a core of a water-soluble substance was shaped into a sphere. Then a waterproof skin of the selected materials was built on to the core and allowed to harden. Then the coated sphere had small holes cut in the skin at the top and bottom poles (these are the regions where minimal distortion is to be expected) and the whole thing was put into water till the core dissolved. The cores were made about 10 cm wide and the skins about 2 mm thick, that is 2% of the diameter. This is similar to the purchased 'playball' and also to many miospores, including *W. lignieri* pollen. Magnesium sulphate, commercial Epsom salts, was found to make a good core. This salt when heated with a few drops of water seems to melt in its water of crystallization and soon boils as a liquid slush. This can be poured into suitable moulds and forms blocks on cooling. The blocks have the consistency of compact frozen snow and they can be sawn into cubes and then shaped with a coarse rasp into spheres. For the skins I used materials whose properties were familiar to me.

Before dealing with the results of the experiments I will discuss briefly the basic principles of the compression of a sphere. When a hollow sphere is flattened by loading from above, the skin at the top is ultimately pressed against that at the bottom to give a disc of two layers, continuous at the edges. This is the primary distortion of compression. But because of the geometric nature of a sphere certain secondary distortions must occur; they are unavoidable but their effects may not be obvious. If we consider such a sphere of radius r its circumference is $2\pi r$ and its surface area is $4\pi r^2$. It may be simpler just to consider the compression of the top hemisphere into a disc of single thickness and for this we have $2\pi r$ and $2\pi r^2$. If we now compress this hemisphere into a circle of radius r then awkward consequences follow; the distance over the top of the hemisphere πr is reduced to $2r$. This factor, $\pi/2$ occurs again and again in this discussion; it is nearly 1·57 to 1. At the same time the area $2\pi r^2$ is reduced to πr^2, plainly a lot of skin must have gone somewhere and it can be taken in various different ways, each being a secondary distortion. Another possibility is for the hemisphere to spread outwards, keeping its distance πr from side to side over the top. Its diameter is increased from $2r$ to πr, that is by 57% of the original diameter.

When such a sphere holds its form, it is because its hollow skin has various mechanical strengths in adequate degree, and when it collapses under a load this happens because one or another of these mechanical strengths has failed, often several at once. It is easier to understand the effects when one strength in particular fails, and for the constructed models materials were chosen such that they should be very adequate in some respects but weak and ready to fail in one particular strength necessary for the maintenance of the spherical form. Provided this failure predominated in an obvious way it seemed good enough to show that the principle applied; it did not matter if other secondary distortions occurred to a slight extent, as they do indeed in some of the experiments illustrated in text-fig. 5.

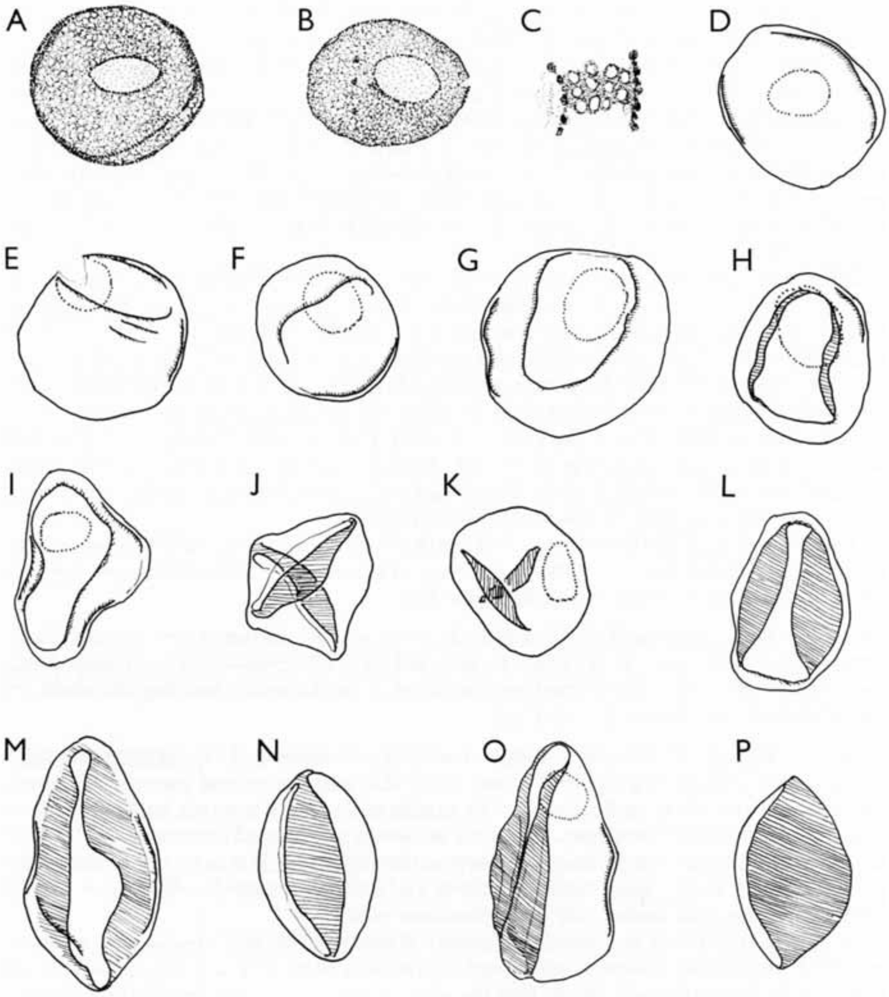
The secondary distortions are of five main groups, each governed by a particular mechanical failure; if others can occur I have not thought of them. I arrange them in order with the most obvious visible effects first.

Failure 1. The skin is rigid and brittle and so cracks and shatters rather than flattens into a continuous disc. This failure is included only for completeness; it may never occur in fossil spores. Such shattering is familiar in the much less flexible shells of lamellibranchs preserved in soft mud.

Failure 2. The sphere spreads to a disc πr wide, an increase by 57%. At the same time the circumference increases by 57% and if the skin will not extend smoothly it snaps and cracks run in toward the centre. The cracks will narrow inwards because there is less stretching in the inner part. But most materials will extend somewhat and so the cracks are neither as numerous nor as deep as they might be. It is to be noted that if the original sphere were a spore with a regularly and uniformly pitted wall, the pits would retain their size and shape over the spread-out wall.

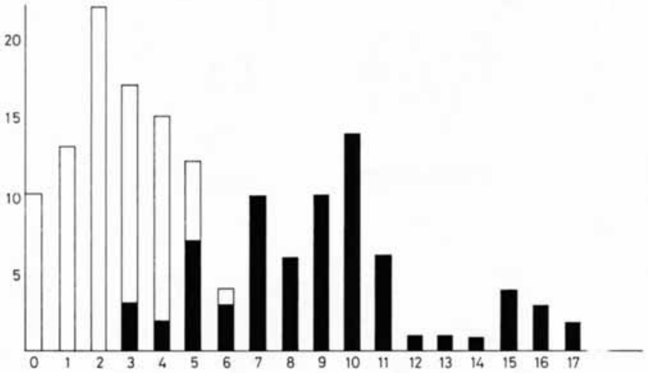
A half grapefruit skin when compressed illustrates this deformation in a hemisphere. For a model, a skin of commercial putty was used. This consists of powdered chalk and a viscous liquid oil. At first the putty is so soft as to be nearly liquid and it can be pulled out without snapping. But in air, the oil oxidizes, 'dries' to a resin and the putty becomes increasingly solid. At first it will still extend somewhat but a few days later it becomes fully solid and will not extend in a plastic way at all. Thus as the properties change putty can be used for different models illustrating different failures.

The putty for this hollow model was allowed to harden for four days. It will be noticed (text-fig. 5A) that while it has split convincingly (it was allowed to flatten under its weight at first and finally pressed gently) one wedge has broken across, shattering.



TEXT-FIG. 3. Pollen grains of *W. lignieri*. A, B, grains with surface ornamentation sketched (pits not drawn individually), ×1000. C, free-hand drawing of edge of grain and of pore (to the left), ×2000. D–P, outline drawings of grains showing the pore (dotted line) and folds, darker parts caused by folds obliquely shaded. In J and N, a pale strip, probably the groove beside the fold is outlined. Several grains have marginal folds. E, F, G, I have folds in the wreath position forming the edge or part of the edge of a broad basin. J, K, crossed folds on front and back. L–P, grains with a deep groove. L, folds symmetrical. M, irregular. L and M, barley-grain form. N, groove to the left of the middle, no fold to the left of the groove. O, groove to the left and running on to the back. P, groove at extreme left and folds extending across to the right. All the grains are from slide 'A' except F, H, J, N, which are from slide 'B'.

Pollen of *W. lignieri* rarely shows such cracks (see however text-figs. 3B and 3E). Very likely no considerable general spreading occurred, and if any did the wall at the perimeter was able to extend. But radial cracks are known in dispersed spores, particularly in very thick walled ones, e.g. *Tasmanites*. No doubt authors studying cracked spores recognized the cracks as distortions, but if they recognized them as caused by peripheral extension following enlargement, they did not say so. I can see no other possible explanation.

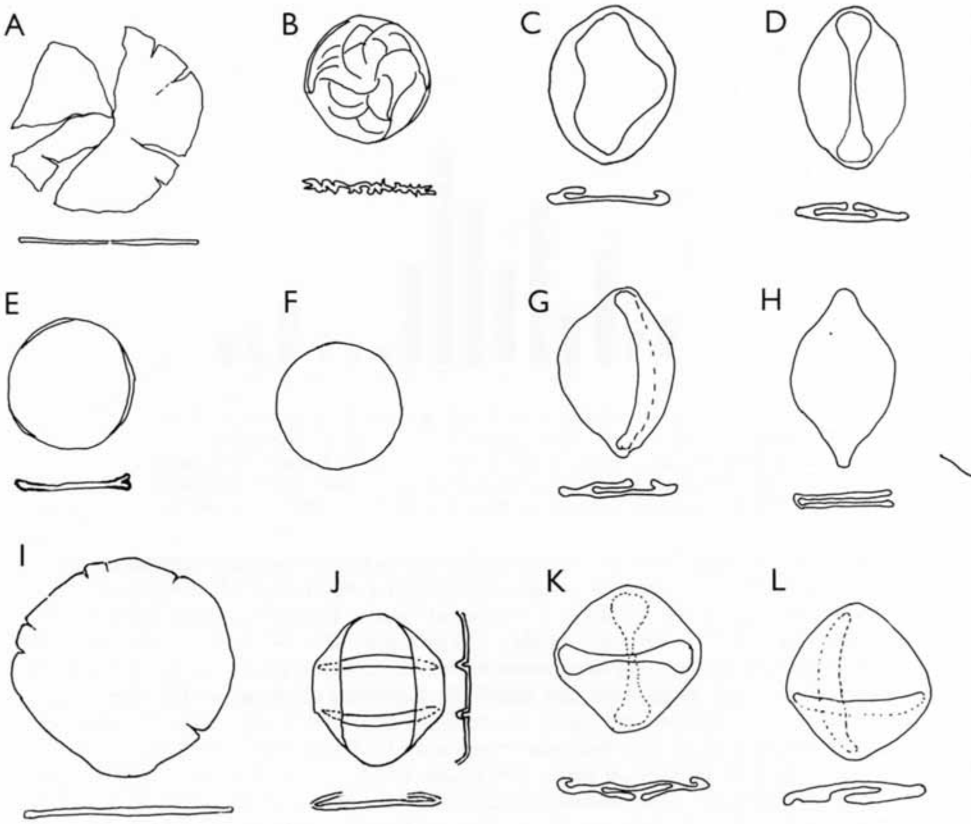


TEXT-FIG. 4. Histogram relating pollen grain shape with surface folds. Horizontal axis difference in μ between grain length and width, vertical columns, number of grains of this shape in a count of about 180. White parts of columns, folds of the kinds that do not cause much change of shape, black parts, folds of the kinds that cause elongation and narrowing. Measurements to nearest 1 μ.

Failure 3: failure by folding. Even if it is adequate in other respects to support a load, the skin of a hollow sphere needs to have some rigidity. A very flexible skin, for instance soft leather, could never by itself form a rigid sphere. Different plastic balls sold in the shops have skins of different rigidity and probably also different extensibility and different compressibility and they varied in the way in which they folded, but by good fortune the first one purchased, the 'playball', happened to show just the effects seen in *W. lignieri*. It also had the merit of resilience and after compression regained its shape for the next trial. The ball was composed of a hydrocarbon polymer.

The most pliant ball tested had a skin constructed of cotton and soft rubber. For a start cotton threads were wound in all directions on to the core (these enable rubber solution to stick to it), and when the rubber had become tacky it was rolled in cotton wool fibres till it would take up no more, let dry, again coated in rubber solution and cotton wool till the dry skin was about 2 mm thick. When the core was removed it proved just able to keep its shape in water but was so soft that it collapsed at once in air. The inextensible cotton fibres round the equator prevented any increase in diameter and the surface was thrown into many small folds. The largest of these were concentric folds at the margin itself and somewhat radial folds curving spirally outwards from the pole, now the centre, to the edge. But there were many additional smaller folds and not all are illustrated in text-fig. 5B. The folds on the two sides were unrelated.

No pollen grain of *W. lignieri* shows a surface crossed by many small folds and I conclude that at the time of compression its wall had rigidity comparable with that of the 'playball'. In that ball the skin is at first very easy to deform, but as a depression deepens the skin becomes more resistant and then as sharper folds are produced by compression it resists intensely. Thus even if the first depressions are so placed



TEXT-FIG. 5. Outline drawings of compressed hollow spheres; all drawn on the basis of the same original size (F). Below each compression is a real or imaginary section. A, failure 2 in rather firm putty. B, failure 3 in a very pliant, inextensible skin (soft rubber and cotton wool). C, D, G, H, K, L various folds, all failure 3 in a single plastic ball; skin resilient and readily forms large and rounded folds but resists small or sharp folds. K, L have two grooves, one on the front (firm lines on one or both sides) the other on the back (dotted). E, failure 4 in an inextensible but compactible skin, chewing gum and cotton. F, the original size of all models. G, H, see above. I, failure 5 in rather soft putty, skin has spread out as in A but has stretched. (Small cracks have formed as in failure 2.) K, L, see above.

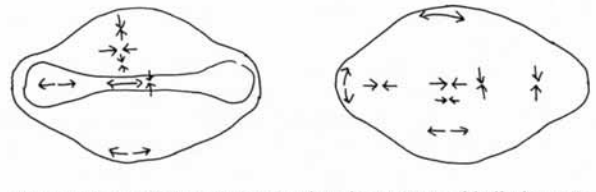
that they should produce several small folds these never develop, but instead one or two large ones are formed.

However, various other miospores both from sporangia and ones dispersed in the rocks show this effect—an almost perfect outline but a wrinkled surface. Most of these are thin walled. An example from the Yorkshire flora is the outer membrane of the pollen grain of *Elatides williamsoni* and of the corresponding dispersed miospore *Perinopollenites elatoides*, figured by Couper 1958 (but he has selected ones which have less folds than usual). Many similar spores have been figured, for example that of *Macrostachya* in Potonié 1962. The feature called 'parallel folds' which these delicate spores are apt to show is discussed on p. 143.

Compression of the 'playball' readily produces a small dimple which on further pressure enlarges to transform the upper surface into a hollow hemisphere inside the lower hemisphere. When this is compressed still more the upper surface forms a cavity with overhanging margins and then the cavity becomes angular with three, four, or five corners. Finally, under heavy pressure the overhanging edges are pressed flat and we have three, four, or five small folds, which I term wreath folds; they are slightly nearer the outside than the centre (text-fig. 5C). Wreath folds (not always a complete set) are common in *W. lignieri* and sometimes it is easy to see that they surround what was a depressed basin (text-fig. 3G, H, I). The flattened ball has now a diameter which is slightly enlarged by up to 10% and its outline is no longer perfectly round, but slightly elongated opposite the longer folds. Instead of a round dimple an elongated one may form and then further pressure makes it into a deep groove. The edges of this groove always overhang but they vary in different compressions, they may be well apart or may meet or even slightly overlap, because of differences in the width of the first elongated dimple. A common form of the ball when strongly compressed is the 'barley-grain' form (text-fig. 5D). When this forms the length of the ball is always increased and its width diminished, and so it is in *W. lignieri* pollen grains (text-fig. 3L–P). The 'playball' was slightly translucent and by transmitted light the groove was pale and flanked by two broad dark folds where two extra layers of wall are seen. The wall is pale again at the edge but not quite as pale as in the groove.

Although this barley-grain form is stable while under pressure, its skin is under considerable stress. These stresses are revealed, if crudely, by making a small slit in the skin. In tension the slit gapes, in compression the edges overlap. By manipulating the slit into different positions the distribution of tensions and compressions is revealed (text-fig. 6). It will be seen that the same piece of skin can be under tension transversely and compression longitudinally and no doubt under strong bending stresses as well. Clearly the net stress is longitudinal extension, pushing the ends of the grain outwards parallel with the groove and at the same time tension drawing in the margins opposite the groove. The length of the deformed ball reaches about 130% of the original diameter and when a slit is made in a part under tension the length at once increases to well over 130%.

The forces concerned pushing out the ends and pulling in the sides are very considerable. When the 'playball' was loaded with 8 kilograms of bricks the ends were thrust outward so strongly in the barley grain form that it took all the strength of my hand to push the ends back. At the same time as the ends were pushed back by hand the bricks were visibly heaved upwards. This outward thrust arises by a sort of lever



TEXT-FIG. 6. Tensions and compressions in compressed ball, the same as in text-fig. 5D. These stresses are displayed by a small slit, diverging arrows indicate tension, the slit gapes, converging arrows indicate compression, the sides overlap. Longitudinal compression occurs also in parts concealed by the folds.

action and the lateral contraction is also powerful. Although the compression and extension forces in the 'playball' are powerful, its skin is not very compressible or extensible and it was difficult to measure any change in the distance between ink spots on its surface. Thus in a fossil spore that behaved like the 'playball', extension would not cause the wall to be appreciably thinner and paler.

The 'barley-grain' distortion of the 'playball' is strikingly like some figures of fossil monocolpate pollen grains but I do not suggest that authors have made mistakes in their interpretation. In *W. lignieri* the distorted pollen grains with a groove flanked by two folds sometimes looked to me very like a true colpus, but often I would have doubted if they were real. I would have been deceived by the most colpus-like forms if I had seen these grains and nothing else.

It is easy to form the first elongated dimple to the side of the middle line and then at first on compression it forms a groove flanked with one broad and one narrow fold (text-fig. 5G), but narrow folds are unstable in the 'playball' and with further compression the narrow one may vanish, some of it going to increase the large fold and some concealed smoothly in intense compression at the side of the groove. It causes the same elongation as the symmetrical barley-grain form. A corresponding form with a single longitudinal fold is the commonest of all in *W. lignieri* (text-fig. 3N, O). The first dimple can be put in a purely lateral position and as before enlarged to form a large hemispherical basin. This on compression takes a peculiar lemon-shaped outline and its length, 140% of the original, is the longest produced by any fold (text-fig. 5H). It is rarely seen in *W. lignieri* (text-fig. 3P), and indeed a purely lateral first depression would seem unlikely to form.

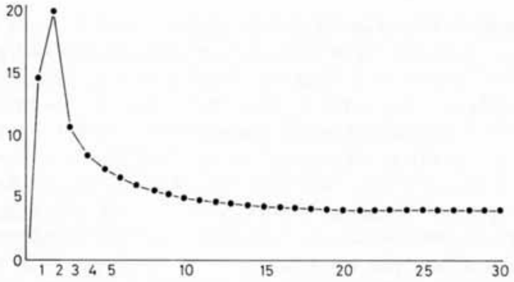
It is easy to impose distortions on to the 'playball' of kinds that it never shows ordinarily, for instance a ring-shaped groove or three parallel grooves but these are unstable and last only as long as they are held. No such forms were seen in *W. lignieri*. As mentioned, the first slight load causes a dimple and the position of this dimple and its round or elongated form determines the final form in heavily compressed distortion. In the 'playball' when compressed between boards the commonest forms were a wide dimple above, leading to wreath folds, or wide dimples above and below which then both became elongated and produced cross folds (text-fig. 5K, L). An elongated groove on the upper side seldom formed, yet in the pollen of *W. lignieri* a groove flanked by one or two folds is the commonest distortion. This difference is not explained.

Other purchased plastic balls gave forms which differed more or less from the 'playball'. One rather harder ball gave very similar forms but the skin proved less able to absorb a small surplus smoothly by elastic compression. When it took the barley-grain form the floor of the groove was at first arched longitudinally and on further pressure this arch was unable to flatten smoothly but the surplus skin formed a small fold transverse to the main groove. In the still harder table tennis ball this effect was even more pronounced and two transverse folds formed (text-fig. 5J). I have not seen this distortion in any Jurassic miospore. The folded forms with a colpus-like groove are discussed later.

Failure 4. The skin fails by permitting itself to be compacted and thickened under pressure and this thickening takes up the whole surplus. The final form is thus a vertical projection of the thickness of the skin at each point; the thickness in the middle is unchanged but considerably increased towards the edge. The precise way the thickness increases depends on the thickness of the skin as a fraction of the diameter and on the position. The following table gives computed figures for successive tenths of a radius measured horizontally from the edge to the centre for a sphere of external diameter 100 mm and internal diameter 98 mm.

1	2	3	4	5	6	7	8	9	10
4·8	3·4	2·8	2·5	2·3	2·2	2·1	2·0	2·0	2·0

It should be possible to recognize the increased thickness of the first tenth in a comparably compressed fossil spore. I also give a graph (text-fig. 7) to show the computed thickness in hundredths of the distance from the edge to the centre, the maximum which is at two hundredths is 19·9: I am grateful to Dr. D. T. Hopkins for these figures. If the skin had been thicker, say 5% of the whole diameter, the maximum would have been slightly further from the edge and there would have been more increase in the second and third tenths.



TEXT-FIG. 7. Compression of a hollow hemisphere of external diameter 100 mm, internal diameter 98 mm. The wall substance is compacted on to the horizontal; the left edge is at 0 and the steps are at 1 mm intervals. At 30 the thickness is 2·8 mm; at 50, the top of the hemisphere, it would be 2·0 mm. Vertical and horizontal scale units in mm. The thickness at 10, at 20, and at 30 correspond to those at the figures 1, 2, 3 in the table above.

The first attempt to construct a model showing this distortion failed. This was the rubber and cotton wool skin but the rubber though very soft was too resilient. So for the next hollow model I tried the least resilient waterproof material I knew as a cement and this was the latex of chewing gum and it proved successful though it was unpleasant to use. It was prepared by boiling chewing gum in water to extract sugar and then the latex was dried and kept in benzene for some days in which it forms a sticky paste. This paste was applied in the same way as the rubber solution and the skin was built up in layers with cotton wool. The hollow ball was softened with warm water and let collapse in air. It gave a disc of the original diameter and without wrinkles except for a minute one at the very edge. The thickness was obviously greater at the edge but the skin had not been even enough for measurements to be worth while. Such a disc would certainly look darker towards the edge by transmitted light and the marginal fold would be visible as a double margin. It was evidently formed because even this wall was not sufficiently unresilient to take the great amount of compaction it needed to take.

This sort of distortion may have occurred in the apparently unfolded round grains of *W. lignieri* but in only a few of these was thickening in the marginal tenth at all obvious. What was, however, to be seen was the double margin, a minute concentric fold right at the edge and evidently caused by the considerable compaction.

Yorkshire dispersed spores were examined for this distortion. Some do show perceptible darkening at the edge and some show a small fold by the edge but many showed neither.

Failure 5. The whole skin is allowed to spread out evenly because while it refuses to compress and shorten in the radial direction, it permits stretching in the tangential direction. Instead of a sphere of diameter $2r$ and with a distance from side to side over the top hemisphere of πr we have a disc of diameter πr. Its perimeter is increased in the same ratio, $\pi/2$. The distortion is the same as in failure 2 except that there is stretching instead of splitting. The increase in the perimeter, 100 units to 157 units, is considerable and the area of the skin has increased. The disc looks altogether larger than the original sphere. At the same time there should be stresses in the skin and a certain thinning towards the edge and surface pits, while unaltered radially, should be extended tangentially. This distortion even if occurring fully would be hard to recognize and certainly unrecognizable if occurring to a small extent together with other distortions. For instance if combined with failure 4, compaction, there might be no change of wall thickness.

Because it is so difficult to observe, it is difficult to say whether this distortion occurs to any considerable extent in compressed spores. It certainly occurs to a small extent in ones showing another distortion, that of failure 2 with cracked margins. In these there should in theory be a vast number of radial cracks running from the edge to the centre but instead one sees a few widely separated cracks which run only a short distance. The cracks are broad at the edge but they narrow and end much too soon and this must be because the stretched wall has pulled out smoothly. A compressed half grapefruit skin shows such stretching and splitting convincingly. For a model to illustrate failure 5 a skin is needed that combines incompressibility with extensibility and this is given by a rather soft putty. The solid part, chalk, is incompressible, but the oil is still viscous and extensible. Text-fig. 5I shows a skin of soft putty which flattened under gravity in air; its diameter is about the theoretical one but the putty was slightly too much hardened and did crack slightly at the edge. Here we have mainly failure 5 but some of failure 2. It is unlikely that this sort of expansion occurred in the present sample of *W. lignieri* pollen. The effect should be maximal in a round grain without visible folds; folds by the margin or wreath folds would have taken the surplus skin. In fact the round, smooth grains are no larger than the others.

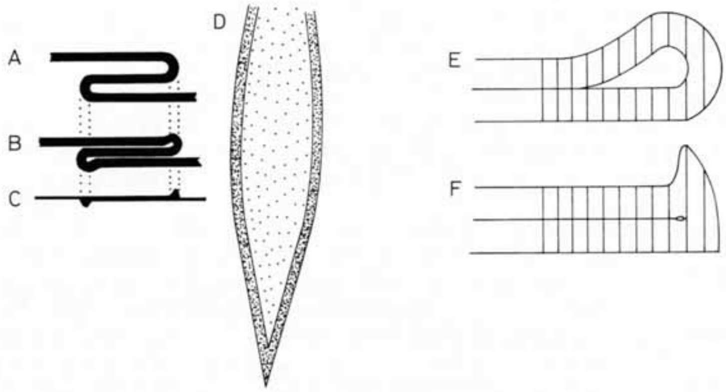
Summary. In the flattening of a sphere, or indeed any solid, secondary distortions caused by the surplus skin are inevitable. These may be of several alternative forms arising from the mechanical properties of the skin. Some of these cause effects which are obviously distortions but others are much less obvious and may be invisible. There is no reason why two or more kinds of distortion should not occur together and probably they do. At most these distortions would increase a spore diameter to 157% of the original but others cause no such enlargement. The spores least likely to have enlarged in this way are ones with a thickly wrinkled surface and ones with a compacted and double margin, but those with a wreath of folds or crossed folds—one front, one back—would not have expanded much. A single strong fold through the middle or a groove and two folds (like a colpus) are likely to cause much extension along the fold and contraction across it.

Parallel folds. Two kinds of distortion may have been called parallel folds. At the side of a groove, whether an original colpus or a groove caused at an early stage of compression, later compression produces two separate folds which are almost parallel, but such folds are normally recognized for what they are.

More commonly the term is used for the two edges of a single, elongated fold. Text-fig. 8A represents in section a simple fold in a spore wall or cuticle. Inevitably this has two edges and text-fig. 8B represents the same fold after moderate compression. On severe compression (text-fig. 8C) adjacent surfaces stick or fuse together. There is commonly also loss of substance, often four-fifths of a cuticle or spore wall vanishes. However, the ridge formed at the sharp bend remains and its width shows the original thickness of the membrane. Text-fig. 8D shows the same fold in surface view; the border is the original thickness and the part enclosed is slightly darker having two additional layers of membrane. In a thick or dark-coloured membrane this is obvious and the fold is recognized as one, but in a thin and colourless membrane it is scarcely darker and the two edges are the 'parallel folds'. A clear polythene bag on which a fold is imposed and then compressed shows this convincingly by transmitted light, only the edges of the fold are recognizable.

Even such a simple fold causes secondary distortions. A strip from the plastic 'playball' was cut and compressed and the fold produced, as seen in side view, is drawn with some accuracy in text-fig. 8E, F.

Note the small ogee shaped cavity, this becomes smaller and comma shaped with further loading. If this form on vertical compression gave a vertical projection of the thickness at each point towards the edge of the fold we would get a double membrane of the form in F, the vertical thickness being considerably increased between the almost obliterated fold cavity and the very edge.



TEXT-FIG. 8. Folds in a membrane. A–C, imaginary membrane with a fold, in section. A has rounded folds, in B the fold is pressed flat, C the same as B after full compression. Much of the substance has vanished. D, the same fold in surface view. The simple fold appears as 'parallel folds' and the edges show the original thickness of the membrane. Light stippling marks two thicknesses of membrane, dark stippling the compressed edge of a fold where the thickness is more than double. E, compressed fold in a strip, cut from the 'playball' drawn to scale. The surface beneath was hard and flat but that above somewhat padded. F, projection of E on to the horizontal.

COMPRESSION OF SPORES IN A MATRIX

The matrix to a large extent controls the distortion of a compressed spore and is thus of the greatest importance but since this is outside the scope of the present study it is treated only lightly. A few experiments on the compression of balls in a matrix were made, however, and these indicated that much more might be done usefully.

The whole of my ideas of compression of plant organs in a matrix came directly from Walton. He told me that he had compressed various solid plant organs—plant stems, apples, and the like in wet sand in a power press so constructed as to allow surplus water to drain away. But he never published his results in detail. Instead he used his findings to reassure himself when he dealt with compression in a theoretical manner (Walton 1936). His general conclusions were simple. A spongy solid such as an apple makes a hemispherical bed in the sand and under pressure it loses water to the sand and this water drains away. The apple presses down into its hemispherical bed and the sand above follows the apple. Thus we have a cup of compressed and dehydrated tissue occupied by a plug of sand. The diameter of the cup is exactly that of the apple. The final form of the 'compression', a term Walton put forward in his paper, is determined by the downward facing side; the top has but little effect. With a compressible matrix, mud, the effect is only slightly different; first the apple is supposed to form a cup and then the apple and matrix together compress, say to a third by dehydration of the mud. The cup becomes a saucer. Walton's theory demands that the compressed tissue should have negligible rigidity (this is reasonable for rotted plant organs) and he supposed that compression in mud took place first in the plant and then in the matrix. But I see no reason why the order should matter, and in my experiments the model and matrix compressed together but with the same effect.

Walton went on to apply this idea to the form of certain Carboniferous plants but I suspect that it was the close study of these plants that aroused his thoughts about compression. I have used Walton's theory many times with Jurassic compressions and always it has proved illuminating. But Walton dealt with a few cases only, all essentially spongy unresilient solids. He did not deal with the spore, a stiff empty skin. We need to study the effect on model spores, that is balls. At first the effect proved the same as that Walton found with spongy solids. Hollow wax balls (constructed round a core—as were other balls) were buried in a matrix, extracted with warm water to remove the core and at the same time to soften the skin, compressed, and finally let cool. In sand the wax formed a hemispherical cup; in compressible lawn-grass mowings it formed a saucer. Plastic balls, some with soft skins, some harder, were compressed in sand, and this time plaster of paris was added to the sand before it was wetted and compressed. When the compressed matrix hardened it was broken open and the ball extracted. There was a perfect hemisphere below while above there was a nearly hemispherical plug pressing down on to the ball. Another compression was made in dry sphagnum moss dusted with plaster of paris, a very compressible mixture. This was wetted before being compressed. The ball gave a mould which was essentially that of a saucer, though the surfaces showed wave-like distortions. There was no expansion that could be measured in this rough experiment. A punctured table tennis ball compressed in sawdust, a somewhat compressible matrix, gave a nearly round cup (Pl. 15, figs. 13, 14). I was convinced that further experiments of similar kinds were unlikely to produce horizontal extension.

It is hard to find a model which will expand horizontally, overcoming the Walton effect of the matrix, but since I was convinced that this does happen to spores, even if rarely, it was necessary to find and understand a model and to consider the forces involved. When Walton compressed a spongy solid, an apple, in sand there may have been no force at all favouring expansion if pressure was applied slowly enough for the juice to drain away. But a spore or a hollow ball with a resilient skin is different and we know that these balls sometimes expand when compressed between flat surfaces in air. A spore can be regarded as a double dome, or for simplicity its top half as a simple architectural dome. A domed roof or indeed any raised roof tends to flatten under its weight and to push the walls outwards. In a roof it may be solved in various alternative ways, by cross ties (but these are not seen in spores), for a dome by a strong chain round its base, and by external buttresses. Our problem is the opposite, to construct a dome which will flatten and push the supporting walls outwards.

Clearly we should choose a situation in which the outward forces develop strongly. The worst situation would be for the ball to be embedded in sand for here the top half simply collapses on to the bottom and no powerful outward forces ever develop. In a matrix we cannot escape the support given to the bottom half of the ball but we can minimize this by using a compressible matrix, for then the bed below our ball becomes a shallow saucer instead of a hemisphere. Then we must use a ball with a rigid skin, resistant to folds of any kind. Once a fold forms it accepts surplus skin and the stresses caused by the surplus skin cease to be available to thrust out into the matrix. Clearly a roof dome of flexible rubber would collapse in folds without pushing the walls outwards. The playball and other plastic balls had a rather rubber-like flexibility and this explains their failure to expand into the matrix. Then to return to the dome supported by a chain, we might cut or weaken the chain. Another kind of collapse could occur (but not in a building made of ordinary materials) by the dome changing its shape, if it changed from a circle to an ellipse it could push out the walls at its ends and drag them inwards at its sides. Finally we could make our external buttresses inadequate. Here are three different kinds of planned failure and two at least happen, as I believe, in fossil spores.

Among the models so far considered the punctured table tennis ball stands out for its rigid skin. But this skin has also great tensile strength and this means that under vertical compression its equator will resist expansion. But we can weaken it—some small vertical razor cuts will do that—and the compressed dome should be able to spread out. Then for the deformation of the dome into an elliptical shape, this might follow if the first dimple on the surface became elongated rather than round. This could be imposed, or left to chance. As for providing a less resistant matrix, I do not doubt that some would resist less than others but the best could not be found without much experiment. All compressible matrices tested became more resistant when compressed, and those which like wet sphagnum or wet cotton wool stay compressed show this unmistakably. The first one used which gave success happened to be dry cotton wool. Very likely another material would have been better. To some extent the table tennis ball avoids this difficulty of consolidation of the soft matrix for under moderate load it collapses suddenly and audibly and further load (my weight) merely led to general compression. The compression of the 40-mm table tennis ball was done in a tin considerably wider than this with a wooden piston that just fitted the tin and there was ample cotton wool above and below the ball. The effects were simple. The compressed ball was always of saucer-shaped contour and this distortion was added to the others. The height of the saucer was about 40% of the original but I believe that this is partly due to resilient recovery and that while under pressure it was flatter. For the same reason the upper surface might not be particularly hollow, but stand away from the lower though under pressure was pressed against it. The lower surface was strongly convex. A ball without any previous treatment became elliptical, 47 mm × 34 mm, that is 117% and 85% of the original diameter. The upper surface has a longitudinal groove of the 'barley-grain' type while the lower has a long shallow groove below one of the bulges on the upper side. This deformation of the under surface is outside what Walton's theory contemplates. There are in addition two small inward folds at the compressed sides which have taken a good deal of skin and account for some of the narrowing. Sharply folded edges have cracked but are not displaced (Pl. 15, figs. 11, 12).

Another ball was weakened by six short vertical razor cuts about 3 mm long round the equator and in compression all these cuts had extended inwards by tearing, the longest gap being 15 mm on each face. The shape is a star with six blunt ended rays. The concave upper surface is mainly smooth but some rays have a deep groove in the 'wreath fold' position and this has evidently taken the surplus skin, for here the rays extend only about 20 mm from the centre, while elsewhere they are 23–25 mm long. The maximum diameter is 48 mm, 20% expansion. The under side is convex and smooth (Pl. 15, figs. 4, 10).

It will be seen that while both balls have extended considerably, the enlargement is a good deal less than the theoretical maximum of 57%. Some must be accounted for by the saucer-shaped form and some must be taken by internal strains. In both compressed balls the perimeter remains what it was, within the accuracy of rough measurement. In spores such deformation would be expected where the wall is strong and rigid and where moreover it keeps its rigidity for a long time after deposition and well into the period of compression of the sediment. And in such spores deformation of the kind giving the blunt rayed star is found, even if only occasionally. It is particularly prevalent in the very thick-walled *Tasmanites*. I will here admit that it was the robust appearance of *Tasmanites* that led me to try the table tennis ball and the theoretical treatment of stresses in a domed roof was supplied after the successful result. But for most dispersed miospores I see no evidence that any spread at all into the matrix has happened and I suppose rather that they have gone through the distortions of a hemisphere and a flattening saucer and so in the end are spared serious alteration of size and shape and even the surface may be scarcely folded. But this is little more than an impression; serious study is needed.

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