THE SEED OF *CAYTONIA*

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ABSTRACT

1. A large number of *Caytonia* seeds has been studied by maceration and the following new parts recognized: inner epidermis and cuticle of integument, nucellar beak forming the pollen chamber and aleurone layer.

2. Certain uncutinized parts are occasionally preserved, through some exceptional process.

3. No cutinized megaspore membrane exists in *Caytonia*.

4. Certain definite parts of the seed are still not understood and call for further work.

5. In having an almost completely cutinized nucellus and no megaspore cuticle *Caytonia* differs from nearly all Gymnosperms except a few fossils, but agrees with Angiosperms. In other respects the *Caytonia* seed is purely Gymnospermous.

INTRODUCTION

THERE have been four accounts of *Caytonia* seeds. The first (THOMAS, 1925) gave the main features, and the next three (HARRIS, 1933, 1940, 1954) added details or gave new interpretations. The present one also adds details and reinterprets, but still our understanding remains incomplete. It was written because a large number of seeds had been accumulated, about 200 of *C. nathorsti* and nearly a thousand of *C. sewardi*, and when they were all examined by maceration, occasional ones were found to show something clearly which most hardly show at all.

Caytonia seeds have been searched for and found in only two floras, the Rhaeto-Liassic of E. Greenland and the Lower Oolitic of N. Yorkshire; but they presumably occur wherever *Sagenopteris* occurs, that is widely, and from the Upper Triassic to Middle Cretaceous. They can be extracted from *Caytonia* fruits but isolated ones are commoner and usually better. They are preserved as coaly compressions and have been studied by maceration and by various methods of sectioning. The Yorkshire flora provides *C. sewardi* Thomas and *C. nathorsti* (Thomas), formerly *Gristhorpia nathorsti* Thomas, the Greenland Lower Liassic *C. thomasi* Harris. The three are taken together, *C. sewardi* being described fully, and then differences of the others pointed out. At the end, doubtful and theoretical points are discussed.

DESCRIPTION

External Features — A typical compressed seed of *C. sewardi* is nearly flat, ovate, 1·5 × 1·0 mm. and when broken across is 0·1-0·2 mm. thick, nearly the whole of this being the seed coats, the interior forms a mere line. A few seeds have other shapes, having been compressed in unusual planes, and these suggest that the seed was originally oval in section and about 0·6 mm. thick. The margins were rounded and seem to have been strong, for they may form ridges over the seed surface. *C. thomasi* may have been similar, but *C. nathorsti* is flatter and its thickness, when broken, is only 0·05 mm. No specimens of it were found which had been compressed lengthwise, but a few have been compressed obliquely and folded. The folds are about 0·2 mm. wide and this may indicate the thickness at the moment of compression (*see* WALTON, 1936). The surface in *C. sewardi* is covered with a network of ridges forming a honeycomb of hexagonal or slightly elongated cells, representing the epidermis of the testa (HARRIS, 1940). The corresponding cells of *C. nathorsti* and *C. thomasi* are longer and their walls scarcely project. The base of the seed shows a flat hilum (rounded in end view in all species) and the apex shows the micropyle where the cells are different, as is described later.

Structure — The middle and base of the seed will be described first and then the micropylar end which is specialized. The parts are described under the following names and in this order, starting from outside:

1. Cuticle and epidermal cells of the testa
2. Outer "palisade" stone cells of the testa
3. Inner "fibrous" stone cells of the testa
4. "Spotted membrane" of testa and, at the base, the "chalazal plug"
5. Inner epidermis and cuticle of integument
6. Cuticle of nucellus
7. Aleurone layer of endosperm

The interpretation of these layers is discussed after they have all been described.

1. Outer Epidermis of Testa ("blow off layer" of Thomas)— This has already been mentioned. Its cuticle is thin and featureless and barely strong enough to cohere even when carefully prepared. The cell outlines which correspond to the very prominent cell walls of the testa are marked by fine lines, sometimes barely visible without phase contrast illumination. The cuticle is similar in the other two species. No soft tissue exists between the epidermis and stone cells of the testa.

2, 3. The Stone of the Testa (*see* Thomas, 1925, Harris, 1933)— These layers form about nine-tenths of the thickness in a seed of *C. sewardi* when broken across. Thomas demonstrated both layers by a method of sectioning which gave good results but with much labour. They can be demonstrated more easily by suitably macerating the seed; the seed is slightly oxidized in diluted nitric acid and then treated for a moment with ammonia. It is washed and teased as the tissues start to swell and dissolve, but the action can be stopped at the right moment by adding calcium chloride. This fixes the wall material and the stone cells will last in glycerine jelly. Ordinarily they dissolve in glycerine even more than they do in water. If the solution is not arrested with calcium, first the middle lamellae of stone cells dissolve, then the thick wall layer by layer and finally the cell content is left as a granular mass with fine projections which filled the pit canals. Even this content may dissolve, especially in glycerine, but it is more resistant than the walls. The outer stone cells (Pl. 2., Fig. 7), which are the palisade layer of Thomas, are a single layer of cubical or columnar cells. Their internal casts are small oval bodies with long, radiating or branched appendages (pits). The inner stone cells (fibrous layer of Thomas) are longitudinally elongated, with square or pointed ends and their internal casts (spicules of Thomas) are rods provided with short arms which occupied the pits. The layer of outer stone cells continues over the whole seed except near the hilum where it is missing. Near the micropyle the cells are flatter. The fibrous cells also continue over the whole seed and are specially numerous near the hilum. Both layers in *C. thomasi* are just like those of *C. sewardi* and both yield internal casts.

The stone is different in *C. nathorsti*. The gap between the nucellus and the outside of the testa is only about 0·05 mm. after maceration as against about 0·1 in the other two and when the unmacerated seed is broken, the substance of the testa is only half as thick. We have until now known nothing about its cells except that they never yield internal casts of fibres when macerated. Thomas obtained no good sections and he makes it clear that the cells in his restoration are surmise; but it now appears that his surmise was right. A seed can be embedded without maceration, and then ground and polished and the exposed surface can be etched It then shows a single layer of cells immediately under the epidermis in a section parallel to the seed surface. These cells are about 20 μ across and have thick walls.

One seed was found to give supporting evidence after maceration. The nucellar cuticle is cracked and many tiny 'dikes' and 'veins' of resin have emerged and penetrate the tissues of the testa. These veins are irregular at first but in the outer layer they constantly form little cylinders at right angles to the surface and usually about 30×10 μ. These are presumed to be resin casts of the outer or palisade cells of the testa (Text-fig. 2). Underneath these cells there is nearly a uniform mass of coal showing nothing definite by polished sections and certainly no fibres such as would be seen in *C. sewardi*. Occasional macerations show cells as internal resinous casts. There seem to be one or two layers of small oval cells, then the membrane called the spotted layer, and then about three layers of small cells. These cells have only been seen at the compressed edges of the seed and there is nothing to indicate that they occur on top of the nucellus. I presume they are absent there.

At the base of the seed there is a small gap in the stone, between the hilum and the chalaza, originally occupied by other tissue. This tissue which is here called the "chalazal plug" is sometimes partly preserved in *C. sewardi*, but is more often and more completely preserved in *C. nathorsti* and *C. thomasi*. It is dissolved on long maceration. In *C. sewardi* this tissue is seen as a confused mass of small cells forming a cap over the chalaza and hiding it. There is not a cutinized membrane, but all the walls of at least one layer of small isodiametric cells are more or less preserved. In *C. nathorsti* the tissue at its best forms a strand running from chalaza to hilum, and again all walls are preserved (Pl. 2, Fig. 9). The inner cells

are elongated, but no other details are visible. The outer ones are a slightly elongated small-celled parenchyma overlapping the chalaza. *C. thomasi* has a chalazal plug like that of *C. nathorsti* (HARRIS, 1933, PL. 5, FIG. 5). In all species the cells of the chalazal plug are preserved in the same way as those of the micropylar collar and are discussed with them later.

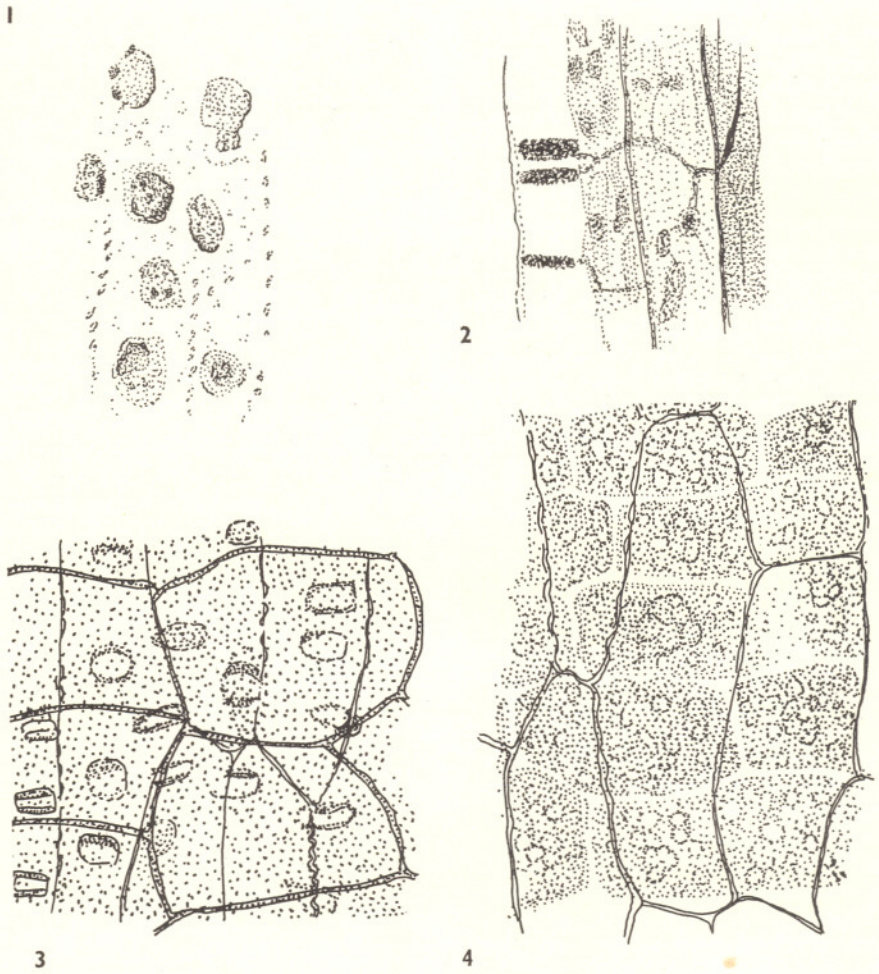
Layer 4, the "spotted layer", has not been reported before. It occurs inside the stone and extends from the middle of the micropylar canal around the inner cuticle of the integument and nucellus which it closely invests and extends beyond it almost to the hilum. It is, however, separated from these cuticles by a film of matter that dissolves on maceration and at the compressed sides extends up to 20 μ beyond the inner cuticle of the integument, which may indicate their original distance apart. It is only seen conspicuously in perhaps 5 per cent of seeds of *C. sewardi* and 2 per cent of *C. nathorsti* from the Gristhorpe Bed, so it is not surprising that it has been missed. A faint trace of it can, however, be found in many seeds, while most *C. sewardi* seeds from some other localities show it clearly. It is well seen in fully macerated seeds but long maceration destroys it, leaving the nucellus.

When conspicuous, the spotted layer is easily seen at a low magnification as a pattern of even-sized and evenly spaced brown spots (PL. 1, FIG. 2), recalling the plumage of a partridge. The spotted layer is supported by the robust nucellar cuticle and was only rarely peeled off as a coherent but exceedingly delicate membrane. The spotted layer varies greatly, even when clearly visible. One extreme form, seen in *C. sewardi*, looks like the internal casts of small round or oval cells without any obviously continuous membrane (TEXT-FIG. 1). Another (seen chiefly in *C. nathorsti* at the edges of the seed) is a delicate continuous membrane without obvious spots. Occasionally also the spots are well developed but after maceration become unconnected and drift about inside the cuticle of the testa. Sometimes the membrane will show conspicuous and regularly spaced spots in one region but in another there are gaps as though the spots had dropped off.

In *C. nathorsti* the spots are usually ring shaped (TEXT-FIG. 3) as they sometimes are in *C. sewardi*, and look like hollow papillae pointing outwards.

5. INNER EPIDERMIS AND CUTICLE OF INTEGUMENT — This layer is never seen alone being inseparable from the cuticle of the nucellus and shows itself as a set of cell outlines superimposed on it. A very few seeds shows the whole epidermal cells (PL. 2, FIG. 8). They form a layer of flat, polygonal cells with very conspicuous walls; or the walls may partly separate when they form flattened oval bags. Normally the cell outlines alone are seen in the cuticle (TEXT-FIG. 3), but most seeds show some traces of these. In a fifth of the seeds of both *C. sewardi* and *C. nathorsti* they are clear and the outlines form ridges projecting outwards. The cells are broader than long (PL. 1, FIGS. 1, 3) unlike the nucellus cells which are elongated and with walls projecting inwards. Although it is never possible to separate this cuticle from the nucellus, it may extend a little beyond it at the compressed sides of the seed, sometimes for as much as 10 μ. This layer is just the same in *C. nathorsti* as in *C. sewardi*. I reported the existence of this layer in *C. thomasi* (HARRIS, 1933) and in the other two species (HARRIS, 1940) but I did not see the cells. At the chalaza one would expect this layer to join the nucellus, but I failed to see the union. Both cuticles become delicate and the inner cuticle of the integument is last seen 20 μ above the end of the nucellus.

6. THE NUCELLAR CUTICLE — This robust membrane has been repeatedly figured but under different names (*see* THOMAS, 1925, PL. 11, FIGS. 12, 13; PL. 13, FIGS. 26, 27; HARRIS, 1926; HARRIS, 1933; present paper, PL. 1, FIGS. 4, 5; TEXT-FIGS. 3, 4). It is the only part of the seed which survives rough maceration and looks almost exactly the same in the three species. It forms an oval sac, flattened in the fossil, but originally open at both ends, and if the beak has been torn off, the two ends are similar, except that it is thicker towards the micropyle. It shows large and often conspicuous elongated cells in rows which converge on the micropyle and chalaza and at these two ends the cells become small and short. The lateral walls project inwards and are usually straight, but occasionally sinuous. The surface is smooth, neither papillate nor pitted, but very occasionally shows ribbing passing in from the side walls (PL. 1, FIG. 4). The chalaza forms a round hole 0·1 mm. wide and here the cuticle is delicate (PL. 2, FIG. 10; HARRIS, 1935, PL. 5, FIG. 6).



TEXT-FIGS. 1-4 — 1, *Caytonia sewardi*, spotted membrane isolated. Some of the spots are missing. × 400. 2, *C. nathorsti*, edge of seed. From left to right, cuticle of integument; 3 resin-filled 'palisade' cells; spotted membrane with obscure cells inside and outside and nucellus (dark membrane in section and surface view. A thin vein of resin has emerged from the nucellus and has invaded occasional cells. × 400. 3, *C. nathorsti*. First layer is spots of spotted membrane (some missing). Second layer is broad cells of inner epidermis of integument. Third layer is elongated cells of nucellus. Fourth layer, aleurone disintegrated to form a homogeneous mass. The cells beneath are omitted. × 400. 4, *C. sewardi*. Elongated nucellar cells overlie granular contents of broad cells of aleurone. The corresponding layers of the other side, visible at a different focus, are omitted. × 400.

7. ALEURONE LAYER — Although this has not been previously reported, both Thomas (1925) and Harris (1933, 1940) observed traces of brown matter which must have belonged to it. Harris interpreted the brown matter as the megaspore membrane. After ordinary full maceration about one seed in twenty of both species shows it clearly as an organized layer, but a good many more show some traces of its cells. In many other seeds the cells have broken down and form a nearly uniform mass. Few show nothing. It is fairly resistant to maceration, but in the end is destroyed before the nucellar cuticle. It is possible, if not easy, to detach the nucellar cuticle from it and this indicates a film of soluble coal between the two, representing some disorganized cell wall material.

At its best, it is seen as a pattern of pale lines delimiting angular brown cells. The

walls are unrefractive, looking pale on accurate low focus but dark on high focus (PL. 1, FIG. 5, TEXT-FIG. 4); the refractive contents are not quite uniform but show unrefractive globules like water drops dispersed through an oil. The cells are isodiametric or transversely elongated and often form indistinct transverse rows, though the underlying cells of the aleurone of the far side may confuse the picture. At the base of the seed the aleurone stops distinctly above the chalaza, so it is not seen exposed. When less well preserved, the cells may round off when the nucellus seems to contain a lot of even-sized brown globules. Very often the aleurone cells run together in transverse rows to make dark bars across the nucellus (cf. THOMAS 1925, FIGS. 12, 13, this paper, PL. 2, FIG. 9). Sometimes all trace of cell structure is lost and the whole nucellus is filled with brown refractive matter.

When well preserved, the aleurone cells stop 15 μ short of the compressed edges of the nucellus and 25 μ short under the micropyle, but when disorganized, the brown matter goes to the edge of the nucellus. In this state it looks like an ill-preserved megaspore membrane and I reported it as one (HARRIS, 1933, 1940), but on re-examining the material I conclude that no seed of any of the species shows a definite megaspore membrane.

The upper and lower sides of the aleurone layer are pressed together and no organic matter remains to insulate them. They adhere tenaciously and have not been separated by maceration. There is no relic of tissue preserved inside the aleurone layer and we know nothing of the inner part of the endosperm or embryo, nor at the micropyle end of archegonia.

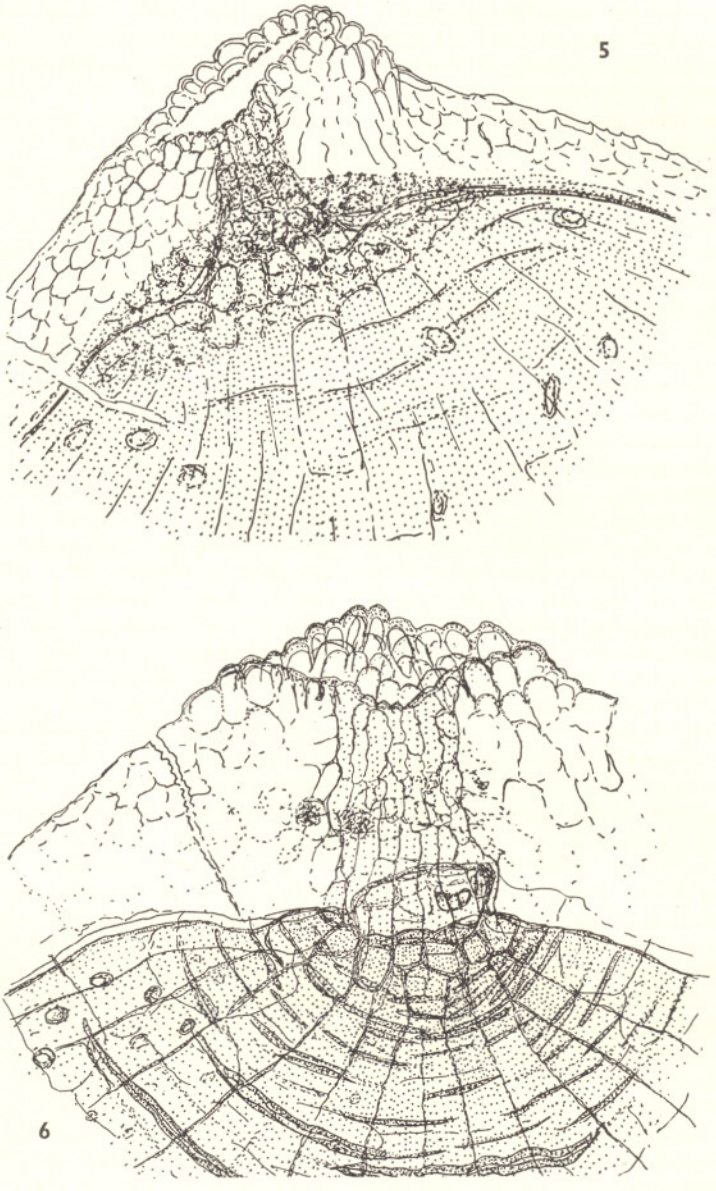
Apex of the Seed — The apex of the seed is often obtusely pointed and the opening of the micropyle is at the very top. The micropylar mouth is flattened in the plane of compression to a closed crack, and vertically or obliquely compressed seeds of *C. sewardi* suggest that it was originally flattened in this plane and may have been closed in the ripe seed. The micropylar canal is quite free from particles of fine mud. In all three species the epidermal cells of the integument are specialized along the two tracts running from the micropyle a short way along the edges of the seeds.

In seeds of *C. sewardi* which have been compressed in unusual planes these tracts of cells can be seen on the surface of the seed. The outer walls of these cells bulge to form a hemisphere or are even higher and the cuticle extends conspicuously inwards along all the side walls. Over the rest of the epidermis it does not extend inwards, and the cell outlines are hard to see. These tracts occur in all three species, but are most conspicuous in *C. nathorsti*.

These specialized, bulging cells around the micropyle were distinguished by Thomas, who regarded them as an inner integument. I made a special study of the cuticle in the micropylar region of both *C. sewardi* and *C. nathorsti* to look for discontinuity. I hoped to see a point where two epidermal cuticles, one with flat and one with bulging cells, suddenly turned inwards and faced one another, but I saw nothing of the sort (*see* TEXT-FIGS. 5, 6). The change from the flat to the bulging cells, though rather rapid, is not sudden but one or two intermediate cells occur. There is often a dip inwards in the seed outline at the sides of the micropyle, as Thomas noted, or there may be a slight obtuse angle here, but the inward or outward angle does not exactly coincide with the change in integument cells as a rule.

I conclude that there is no morphological boundary but only a single epidermal layer which is specialized near the micropyle. At the mouth of the micropyle the same cells occur, but the epidermis dips in to form a broad, flattened funnel.

It is easy to prepare the cuticle of the micropylar canal (*see* THOMAS, 1925; HARRIS, 1933, 1940). The seed should be thoroughly oxidized and then put on a slide and the maceration should be completed in the minimum of ammonia. If it is manipulated or if it is moved about in fluids, the micropylar canal cuticle is sure to be torn as it is all that remains to connect the inside and the outside of the seed. In *C. sewardi* and *C. thomasi* it is about 150 μ long, and 70 μ wide, but usually a little shorter in *C. nathorsti*. The cuticles of the upper and lower sides are inseparably fused and about 1 μ thick. The cells are strongly marked because cutinization extends back along the whole lateral walls. In *C. sewardi* and *C. thomasi* it shows nearly isodiametric cells, but in *C. nathorsti* they are about twice as long as broad. At its base it fits closely over the beak of the nucellus, but it is easily torn away here, either removing the beak (as most commonly



TEXT-FIGS. 5, 6 — 5, *C. nathorsti*. The micropyle is occupied by a little fine mud (left white). The lower part of the micropyle canal and top of the nucellus are concealed by collar tissue. The micropylar cells seem to pass gradually into the ordinary ones of the testa. A few of the spotted layer spots remain. × 200. 6, *C. nathorsti*. The micropylar canal is rather long and fits over the short open beak and probably continues as the inner epidermis of the integument. There is a pollen grain at its base. Concentric ridges are probably folds in the disintegrated aleurone layer. A little of the spotted layer is seen on the left but elsewhere is missing. × 200.

Both seeds are compressed in the usual plane and a good many cell layers visible at different planes of focus are omitted for clearness.

in *C. sewardi*) or tearing from it (*C. nathorsti*).

About a quarter of the seeds of *C. sewardi* and half those of *C. nathorsti* show a tissue around the middle or base of the micropylar canal which I call the "micropylar collar". It is enclosed by the stone and is immediately inside the "spotted layer". Thomas (1925) figured it (PL. 11, FIG. 11) as a possible inner integument. In *C. sewardi* the collar is a conical mass of small, round cells of more than one layer and with all their walls more or less preserved in the best specimens. More commonly the cell walls are preserved unevenly and there is just a confused mass hiding the base of the canal. In *C. nathorsti* (PL. 2, FIG. 6, TEXT-FIG. 5) the tissue is more elaborate. There is a layer of rounded cells with more or less complete walls across the base of the micropyle and several layers at its sides. This collar tissue extends outwards along the margins of the seed, just inside the stone and its cells become elongated. Less of this tissue is seen as it is followed back and it was only rarely traced much beyond the middle of the seed, usually being lost near the front. These downward extensions are only seen at the compressed sides of the seed. There is none of the tissue in front of the nucellus.

Two seeds of *C. nathorsti* show some clearly preserved tissue above the 'collar', occupying the space at the sides of the micropylar canal which happens to be rather long. This tissue again only exists along the flat edges of the seed and there is none on top of the micropyle. It consists of about two layers of oval cells 40 × 20 μ with completely preserved but thin walls. Just outside them there are some solid oval bodies of half this size, looking like internal casts of small cells.

This tissue above the collar is not the same as the rows of elongated cells or septate tubes which Thomas showed in his reconstruction of *C. nathorsti* lying alongside the micropyle. I have seen a few seeds which, after maceration, suggest just such elongated cells, but I believe the cells are all epidermal and indeed two different kinds were perhaps embodied in the restoration. In some seeds the cutinization of the anticlinal walls of the epidermal cells at the mouth of the micropyle extends back a remarkable distance, occasionally 50 μ and forms delicate unseptate tubes almost parallel with the micropylar canal and close to it. In other seeds the ordinary epidermal cells of the testa form rather conspicuous longitudinal rows near the apex of the seed and their crushed cuticles show the longitudinal walls conspicuously, but the transverse faintly. They form obscurely septate cell rows like his figure, but they are external and not really close to the canal. It should be possible to trace the cuticle of the micropylar canal down over the nucellus where it would become the cuticle of the inner epidermis of the integument. In a few seeds (TEXT-FIG. 6) this may be possible, but it is far from clear. In most seeds the top of the nucellus is so thickly cutinized that it is impossible to see whether any delicate cuticle exists outside it.

The nucellus is often flat or slightly hollowed near the seed apex, but just below the micropyle it is suddenly raised to form a short nucellar beak (this beak is the same as what Thomas called the plinth of the megaspore). In *C. nathorsti* the beak is usually large and conspicuous, being thicker walled than the micropylar canal which fits round it (THOMAS, 1925, PL. 11, FIG. 11), but it may be short and hardly distinguishable. In *C. sewardi* it is smaller and less thick walled, but I believe generally present, unless torn off with the micropylar canal. *C. thomasi* seems like *C. sewardi*. The apex of the beak is uncutinized and forms an open hole, and it must have been open in life, since in suitable preparations of all species pollen grains are to be found inside the beak, just below its base.

The cells of the nucellus converge on to the beak, and as they approach it, become more thickly cutinized on both surface and side walls. At the base of the beak the cuticle is very thick and forms a dark brown mass in which it is hard to see details, unless maceration is long continued. At the beak, the cuticle becomes rather less thick again (especially in *C. sewardi*). In both this and *C. nathorsti* I convinced myself that the beak is the true upward continuation of the nucellus. In both species the beak is round in section.

Pollen grains agreeing with *Caytonanthus* have been seen repeatedly in seeds of all the three species. They are best shown by macerating seeds rather fully and then clearing them with ammonia carefully on a slide. The main difficulty is that the grains are hidden by the dark nucellar cuticle, since nearly all are at the base of the beak.

Just below the micropyle the aleurone layer is separated by a slightly wider gap

from the nucellus than it is at the sides of the seed. Its cells are rather hidden by the dark cuticle of the nucellus and seem a little smaller than usual. It was impossible to tell whether any gap in the aleurone layer, such as is shown in the present restorations, occurs below the nucellar beak.

DISCUSSION

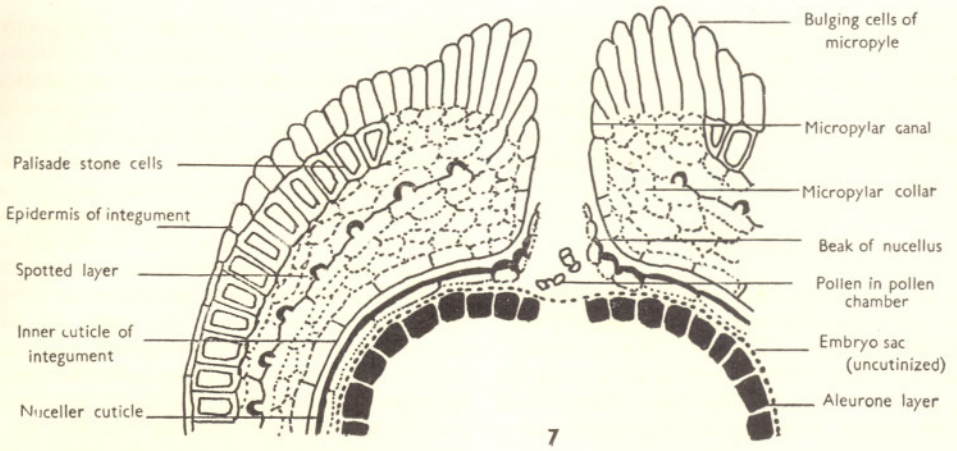
1. THE GENUS *Gristhorpia* — Thomas decided that the differences between the two Yorkshire species, *sewardi* and *nathorsti* warranted their generic separation and he instituted the genus *Gristhorpia*. Since then we have learnt more about the leaves and about the microsporophylls of the two species and they prove very similar. A third species *C. thomasi* has been found and again the other organs are like corresponding ones of the others. Its fruits and seeds are like *C. sewardi* in some respects and *C. nathorsti* in others. Most of what were supposed to be generic differences between *C. nathorsti* and *C. sewardi* proved on further study to be ones of relative size and shapes of closely corresponding parts and thus of specific rather than generic value. One difference of those Thomas gave still survives, and that is in the seed; *C. nathorsti* has no fibrous layer but the other two species have one. I judge this difference too small to make useful generic separation and accordingly *nathorsti* is included in *Caytonia*. This follows what Harris proposed earlier (1940) but with rather less evidence.

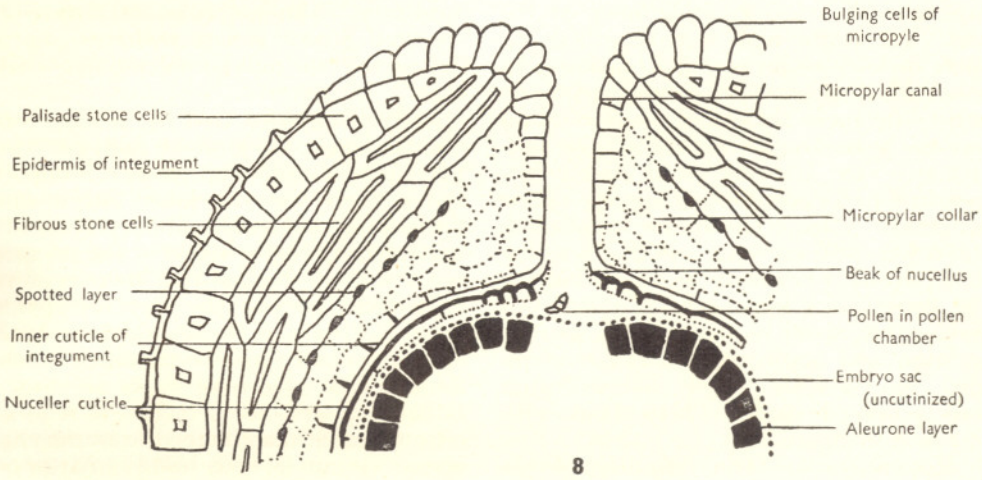
2. MORPHOLOGY — The restorations of the *Caytonia* seeds given by Thomas (1925), by Harris (1933) and the present ones (TEXT-FIGS. 7, 8) illustrate the growth of our knowledge and changes in our ideas. The changes in 1933 were a greater emphasis on cutinized layers; a single integument is shown instead of two; pollen has been seen in the micropylar canal and the nature of the cuticle of the (free) nucellus has been realized. Too few delicate cells were shown inside the stone of the seed and a new error is the interpretation of the decomposed aleurone as a megaspore membrane. In the present restorations the cuticle of the testa is shown on the outer wall of the epidermal cells; pollen is shown in the pollen chamber of the beak of the nucellus; many more delicate cells are shown inside the stone; the inner epidermis of the integument (rather doubtfully recognized in 1933) is now seen clearly; the cells of the aleurone layer are recognized. The cuticle of the megaspore is abolished.

The morphological identification of several parts of the *Caytonia* seed is secure, but of others is by no means self-evident. The nature of some can be guessed from their resemblance to part of a recent seed (though of an unrelated plant) and still others must be left open. This last part of the work on the *Caytonia* seed is plainly unfinished.

The epidermis of the integument or testa, its stone cell layers, its micropyle and hilum seem secure facts of observation. The parts called the micropylar canal and the nucellus with its beak and chalaza and also the inner cuticle of the integument, which are all identified by comparison with living seeds, seem almost as secure. The aleurone layer is perhaps less safe, though identified in the same way. The morphological nature of the 'spotted layer' is left entirely open as is that of the 'micropylar collar' and 'chalazal plug'.

I have concluded that the testa is formed from a single integument and not two as Thomas believed. The question is important and if there were an inner integument, it would offer a possible interpretation of the spotted layer and perhaps of the micropylar collar also. I decided that there is no inner integument because the way the epidermis seems to behave at the micropyle excludes it, but no doubt I could be mistaken in what I think I saw, since the parts are tiny and rather difficult to see. If there were an inner integument, it must extend from the chalaza up to a certain level: it could end at or below the bottom of the micropylar canal or part way up the micropylar canal, or it could form the whole canal and micropyle and end just outside the seed, as Thomas believed. I know no fact in favour of an end below the micropylar canal, but this cannot be excluded. An end opposite the micropylar canal is ruled out because it would mean that the lower part of the canal would be formed by the inner integument and the upper part by the outer integument, and there would be discontinuity in the cellular lining of the canal. There is no discontinuity. The last possibility that it forms the whole micropyle is more serious as there is a change in the epidermis just outside the micropyle, as Thomas made it clear and emphasized in his restorations. The epidermis of the micropyle is formed by bulging cells, but a short way from it they give way to flat ones (in





TEXT-FIGS. 7, 8 — 7, Restoration of micropylar part of *Caytonia nathorsti*. 8, Micropylar part of *C. sewardi*. × nearly 200. Firm lines represent cutinized walls and other firm parts; dotted lines represent parts which are obscure or not seen at all. Both seeds are compressed in the usual plane and the tissues are those seen at the edges of the seed. In a longitudinal section at a right angle to this some of the tissues would be less developed or absent.

C. nathorsti and *C. thomasi*) or hollow ones (in *C. sewardi*). The difference is visible before maceration, but plainer after. At the sides of the seed the change happens at about 200 μ from the micropyle, but above and below it happens at its edge.

The change in the cells is rapid but not perfectly abrupt, and at the compressed edges of the seed there are about three transitional cells, and on the surface one or two such cells (TEXT-FIGS. 5, 6). I have never seen the two cuticles suddenly bending inwards or overlapping the other, or anything suggesting that, and though there is often a change in the seed outline, a bulge or a hollow at about the same level, they do not exactly coincide with the change in the epidermis.

Layer 1, the epidermis of the seed, is shown as a clear epidermis in my restorations, but it was not at first regarded as an epidermis, or at least not an ordinary one. Thomas called it the " blow off layer " and compared it with the outer layer of certain Palaeozoic

seeds called by that name. He believed that its outer wall was lacking, and that its cuticle lined the inner wall. Harris (1940) showed, however, that it was in the ordinary position, but that in *C. sewardi*, where the outer wall has collapsed on to the floor of the cell, it has taken the cuticle with it, so it is seen on the floor of the cell in section. Many recent seeds have a pitted surface formed by sunken epidermal cells.

The abrupt end of the epidermis and cuticle at the hilum is as expected but the change in the character of the cells at the micropyle is not explained. The thinness of the cuticle of the testa of *Caytonia* is perhaps significant for it is usually thick in Gymnosperms and thin in Angiosperms. This may be related to the enclosure of the seeds of *Caytonia*, but in most Gymnosperms the seeds develop in nearly full shelter. The cuticle of the micropylar canal continues the bulging cells of the mouth of the micropyle. It matches the micropylar canal of most Gymnosperm seeds but its cells are more strongly marked than usual because cutinization extends inwards along side walls. It is fully as thick as the outer cuticle of the integument. It is unlike the micropylar canal of normal Angiosperm seeds where scarcely any cuticle exists.

The cells of the micropylar canal continue in an unbroken series to the base where it closely overlaps the cuticle of the nucellar beak and since it fits closely, pollen grains going down the micropyle would not be able to escape into the space between the nucellus and the integument. I have seen a few spores on the surface of the nucellus but they are outside the inner cuticle of the integument and I feel sure they had penetrated from outside through cracks in the fossil seed. None of these stray spores is of *Caytonanthus*.

Thomas fully recognized the natures of layers 2 and 3 forming the stone of the seed in *C. sewardi* and also of their internal casts which he called spicules. We do not know why such casts should be formed, but about 25 per cent of the seeds show them clearly and 25 per cent indistinctly, the rest not at all. It is the presence of the casts which needs to be explained, not their absence, for they are not seen in most other fossil seeds. The preservation of these and of some other uncutinized parts is discussed later.

Layer 4, the spotted layer, is not satisfactorily understood. It seems to have a very delicate continuous membrane just like a thin cuticle (but cell outlines have not been clearly seen) and the spots occur on this, often in longitudinal rows. The preservation of this membrane and of the spots seems independent, and it is rare for both to be clearly preserved. Well-developed spots in *C. sewardi* (where they are commonly solid) look like solid epidermal papillae or alternatively internal casts of small, thick-walled cells. The spots of *C. nathorsti* are commonly hollow and look like hollow epidermal papillae pointing outwards and it seems hard to account for their shape which is that of an open-mouthed sac on any other basis. I have represented them as epidermal papillae in my reconstruction but I am not satisfied that this is right. In particular it fails to account for specimens in which the membrane is coherent but some of the spots have apparently become detached (TEXT-FIGS. 1, 3, 5, 6). Whatever its nature, it was clearly a definite part of the original seed.

Layer 5, the inner epidermis and cuticle of the integument, was identified by its resemblance to this layer in various Gymnosperm seeds. In Cycas, for example, the free part of the integument was an inner epidermis and a delicate, inward-facing cuticle and the nucellus has an epidermis and a delicate outward-facing cuticle. Where the integument and nucellus are adnate (" fused "), the two epidermises join and below that there is no cuticle at all. In the similar fossil, *Beania*, the two cuticles have been pressed together and have adhered inseparably to form what is in effect one cuticle with two sets of cell outlines, which can be seen to become united where the cuticle ends below. At the sides, the integument cells project a little beyond the nucellus, and at the top they continue up as the micropylar canal. It is just like this in *Caytonia*, except that continuity with the nucellus below and the micropyle above was not fully demonstrated. However, in support, there is the fact that the boundary walls of the integument cells project outwards, and of the nucellar ones inwards. As mentioned, in a few specimens the whole anticlinal walls of these cells are preserved, making them conspicuous.

Layer 6, the cuticle of the nucellus, was described by Thomas under the name " megaspore membrane ", but later recognized as the nucellus (HARRIS, 1933, 1940, 1954). Perhaps it was at first regarded as the megaspore because it is the innermost cuticle, but its characters are those of the nucellus of recent plants, especially Angio-

sperms and not those of a megaspore membrane. In the ripe seeds of nearly all the Angiosperms I have macerated (belonging to a good many families) the nucellus has a well-developed cuticle extending from a small chalaza over almost the whole surface and thus nearly enclosing the embryo sac. It has no obvious perforations and the cells of the nucellus have a flat outer wall and the cuticle extends well into the anticlinal walls, making obvious cell outlines. Of course, no pollen chamber (Thomas's plinth) exists in the apical part of Angiosperms, but this organ is to be seen in most fossil Gymnosperms, where it is often like that of *Caytonia*. The greater thickness of the cuticle of the top part of the nucellus is a feature of many Gymnosperms and of some Angiosperms; I do not know its meaning.

Thomas, it is interesting to note, recognized and named the chalaza and nucellar cell outlines and suggested that the beak or " plinth " was an ancestral pollen chamber, though he had seen no pollen in it. His restoration of *C. nathorsti* shows it more or less open above and in all this he foreshadowed its interpretation as nucellus. He regarded this " beak " as a " fairly constant feature " of *C. nathorsti* but absent in *C. sewardi*. I would say it is merely larger and less easily pulled off in *C. nathorsti* than in the other two species. The cuticle of a megaspore membrane is quite different. Angiosperms in general have none, but it is well-developed in nearly all recent and fossil Gymnosperms, with exceptions given later. It is a rather thick sac of cuticle, essentially non-cellular (or a single enlarged cell) and does not usually show any imprint of the adjacent nucellar cells. It has no chalazal opening and only the most minute archegonial openings, not ordinarily seen in fossils. It is almost evenly thick and is covered with small granules which are the end views of minute rods.

It is often hard to see the pollen grains at the bottom of the pollen chamber in *Caytonia* because the nucellar cuticle is so thick as to conceal them.

However, a good many seeds of all three species show them and all the grains seen clearly in this position are *Caytonanthus*. A very few other grains have been seen in micropyles, or outside micropylar canals, having, I think, penetrated cracks in the fossil. Since pollen occurs inside the micropyles of the seeds, *Caytonia* is technically a Gymnosperm, in spite of its nearly closed fruits. Its claim to be regarded as close to the Angiosperm ancestors thus seems less insistent than formerly, but the claim stands nevertheless.

If *Caytonia* had a cutinized megaspore membrane like most Gymnosperms, it would surely be seen and I emphasize its absence even though it may in general be dangerous to build on what a fossil does not show. It is true I reported vestiges of such a membrane (HARRIS, 1933, 1940), but I now realize this was the aleurone in an ill-preserved state. The best seeds show nothing resembling such a membrane.

Layer 7, the aleurone, is clearly the refractive and oily contents of a single layer of cells, but there is nothing to show that it is inside the embryo sac. There is a minute amount of soluble matter between the aleurone and the nucellus, but there is never any within the aleurone and it is impossible to separate the upper from the lower layer of aleurone cells in the compressed seed. Nor is there any suggestion of more than this one layer lining the nucellus, so it looks as if no solids at all remained inside the aleurone at the time the seed was crushed. The aleurone layer is single and not just the outermost layer of a massive endosperm.

No seed *Caytonia* shows anything suggesting archegonia or embryo. This calls for no explanation as their absence is normal in compressed seeds of Cycads and Conifers which doubtless possessed embryo and a massive endosperm too at the start of preservation. It is gratifying when a compression shows anything at all of its inner parts.

While the various cell layers that have been recognized must make up nearly all of the thickness of the testa, there may be layers of delicate cells inside the stone of which we know nothing. We do know of the existence of certain uncutinized layers because there is a film of coal between the cuticles which dissolves on maceration and because successive cuticles may stand a little apart at the compressed edges of the seed. There is nothing to show how many cells are involved and in general my restorations show the minimum. No vascular tissue has been seen in the seed and none is shown.

The gap of about 10 μ between the aleurone cells and the nucellar cuticle is shown in the restorations as occupied by the nucellar epidermal cells and the imaginary embryo sac or megaspore wall. The gap between the

nucellar cuticle and the inner cuticle of the integument is, however, unoccupied since there is no coal between them. Between the inner cuticle of the integument and the spotted layer, two cell layers are shown in *C. sewardi* but more in *C. nathorsti*, where there is direct evidence that they exist. The spotted layer is shown as a layer of papillate cells with a delicate cuticle, and another layer has been put between it and the stone, perhaps gratuitously.

3. *The Preservation of Uncutinized Parts* — As has been noted repeatedly, certain uncutinized parts of *Caytonia* seeds may be preserved but this preservation is inconstant, or even very exceptional. These are the tissues called the ' micropylar collar ' and ' chalazal plug ' and in *C. nathorsti* tissue above the micropylar collar and also small cells underneath the spotted layer. In both species there is the aleurone tissue. In many seeds of *C. sewardi* internal casts are preserved in both layers of stone cells and in a very few seeds the whole cell walls of the inner epidermis of the integument are clearly seen in a macerated seed. We need to know why all these parts should sometimes be preserved.

I suggest that the explanation of the ' micropylar collar ' and the ' chalazal plug ' is that after the seed was buried and its tissues died, oil moved out from the two small openings of the cutinized nucellus, the beak and the chalaza and penetrated the adjacent parenchyma around the micropyle and the chalaza. Here it either lined the cell walls fairly evenly or collected chiefly in intercellular spaces. If such movement occurred, it was not, however, gross injection such as is seen in Text-fig. 2, but a molecular diffusion. The oil then hardened into a resin more resistant to oxidative maceration than the coal formed out of cellulose and lignin, but slightly less resistant than cuticle.

Where the intercellular spaces were chiefly filled, the tissue is seen as a network with solid nodes as is commonly found in *C. sewardi* but occasionally in *C. nathorsti* and where the whole cell is lined, the walls are sometimes complete and the cell looks like an ordinary parenchyma cell. The inner epidermis of the integument is sometimes preserved in this way, and sometimes, too, the cell linings have contracted so that the cells are rounded sacs. In a few seeds of *C. nathorsti* the cells of the collar region are preserved differently, as little oval blocks of granular matter like internal casts. Similar casts occur in a few seeds both underneath the delicate spotted membrane and just outside it, and also in the spaces above the collar and around the chalazal plug.

This explanation is supported by a few exceptional seeds of *C. nathorsti* which show ' vertical dykes ' of resin exuding from cracks in the nucellar cuticle extending right through the testa. This resin is only a little less resistant to maceration than cuticle. One seed has been mentioned in which numerous small resin veins have penetrated individual cells. In another seed large masses of resin occupy its compressed margins, dying away near the micropyle, and where the resin is less abundant, the cellular tissue of the micropylar region is preserved exceptionally clearly.

I suggest that the internal casts of the stone cells of *C. sewardi* were formed from their original contents and are not an invading material. They are unconnected with the contents of the nucellus and the preserved fossil contents seem chemically different from that of the chalazal plug, micropylar collar and the resin veins exuding from the nucellus. When moderately macerated, the stone cell casts are very apt to dissolve in glycerine unless fixed with calcium cations. The micropylar collar tissue and the chalazal plug do not dissolve in glycerine.

I have experimented with the stone cells of the coconut, where there is a dark brown substance occupying the cell interior. When macerated, this substance proves more soluble than the lignified cell walls; but when the nutshell is gently roasted, it becomes much more resistant. Then on maceration the contents remain as isolated internal casts, armed with projections which originally occupied the pits, exactly as in *C. sewardi*. Also as in *C. sewardi* the casts slowly dissolve in glycerine or in dilute alkali. The fossil seeds have not been roasted, but the process of compression over a long period might produce a similar chemical change. I imagine that those seeds which do not produce casts had undergone some preliminary decay which destroyed the contents and the fact that the casts of the outer cells are less often seen than those of the inner ones suggests that this might be atmospheric oxidation.

I would compare the aleurone cells to the green oil containing cells under the nucellar membrane of *Cucurbita*. The best preserved aleurone cells are solid blocks of refractive oily cell contents containing dispersed water

drops. The material is very resistant to maceration, and the oil may well be the origin of the resinous veins emerging from cracks in the nucellus of certain seeds and also of the resinous matter which preserves such tissues as the micropylar plug and the nucellar collar.

It is rare for uncutinized parts of plant compressions to be preserved through maceration but some examples are known. There is the seed *Allicospermum retemirum* (HARRIS, 1944) in which the intercellular space system of the stone is preserved as a 3-dimensional network of rods. A few leaves such as species of *Ptilophyllum* and of *Sagenopteris* may show their palisade and spongy mesophyll cells and in *Pseudoctenis oleosa* Harris (1950) so much of the mesophyll is preserved that it is hard to separate the cuticles. An aleurone layer, very similar to that of *Caytonia* is preserved in the isolated seeds described by Pant (1958); and traces of them seem to exist in *Wielandiella* (where they have not been described) and in *Elatides* (HARRIS, 1943a).

I cannot account for the spotted layer satisfactorily on these lines because it often looks like a true cuticle; it has only its inconstancy of preservation in common with these other tissues.

4. *General Comparison* — Most seeds, living and fossil, have cuticles which place them in one of two groups. On the one hand we have the majority of Gymnosperms (Cycads, Gingko, Conifers, Pteridosperms) in which the megaspore has a strongly developed granular cuticle and the nucellar cuticle is thin and often covers only part of the megaspore. On the other hand, we have the type widespread and perhaps normal in recent Angiosperms in which the embryo sac has no cuticle at all but the nucellus is strongly cutinized and almost covers the embryo sac, apart from a minute chalazal gap. Thus in each there is a single almost complete cuticle deep in the seed coat.

There is evidence in a few Angiosperms that the nucellus has limited permeability of a remarkable kind, but I know of no work on Gymnosperm seeds. However, I suggest that these cuticles in both great groups are more likely to be organs performing functions today than surviving functionless vestiges of free megaspore walls or of free megasporangia.

In this respect *Caytonia* seeds are like Angiosperms and differ from the Gymnosperms mentioned. They deserve full and careful comparison with Angiosperms, but this is not attempted here because to do so would take many years' study; I have merely compared them with a few chosen at random.

We know a few other fossil Gymnosperms which agree in this respect with *Caytonia* and the Angiosperms. The most similar are the isolated mesozoic seeds *Amphorispermum* (HARRIS, 1932, 1943b) which, however, are so like *Caytonia* in all respects that they may represent otherwise unknown species of that genus. They do not help us to understand *Caytonia*.

The seeds described by Pant (1958) as *Spermatites crystallinus* and *S. tetrapterus* from African Glossopteris beds of Permian age are more interesting, particularly because they may well belong to *Glossopteris*. In them also, the nucellus is well cutinized and complete, apart from a minute chalaza and there is no megaspore membrane. As in *Caytonia*, the nucellus bears the imprint of the adjacent inner epidermal cells of the integument. They agree further in possessing cells like the aleurone of *Caytonia* and in having a delicate cuticle round the testa. In other respects they differ or perhaps are merely not well enough understood to be properly compared with *Caytonia*.

The most similar seed in a classified fossil is that of *Wielandiella* first seen by Nathorst at the beginning of this century, and discussed by Harris (1932, 1954). Here, again, the integument is thinly cutinized, but the nucellus is thickly cutinized and it bears the imprint of the adjacent cells lining the integument. Its chalaza is minute and there is no cutinized megaspore membrane, but there are traces of aleurone-like cells. Other Bennettitales are less similar and there must be a great range of seed structure among them but in none of those studied by maceration is there a megaspore of the Cycad type.

Other features of *Caytonia* are distinctly Gymnospermous and not Angiospermous. There is the apparently single integument (most Angiosperms have two); and more important, the well-cutinized micropylar canal, a feature of perhaps all Gymnosperm seeds and absent, so far as I know, in Angiosperms. The nucellar beak, forming a pollen chamber, is by definition non-Angiospermous, but is found in most Gymnosperm orders.

The seed of *Caytonia* shows a mixture of the features of Angiosperms and of various Gymnosperm orders, so indeed do its other

organs. They suggest phyletic relations and at the same time baffle attempts to relate, except at the cost of shutting the eyes to unexplained differences. We may hope that with further knowledge differences may be understood and found unimportant and the numerous Gymnosperm orders, which are so tiresomely separate in the classification of today, will be conveniently and convincingly linked.

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EXPLANATION OF PLATES

PLATE 1

Caytonia sewardi

1. Edge of nucellus showing broad cells of inner epidermis of integument and fragments of spotted layer projecting beyond it. × 400.

2. Spotted layer covering nucellus and projecting beyond the chalaza. × 200.

3. As Fig. 1, but inner epidermal cells of integument broader and spotted layer less distinct. × 400.

4. Nucellus, no other cell layer preserved. Short ridges project inwards from the lateral walls. × 200.

5. Nucellus and aleurone. In the lower part (deep focus) the broad aleurone cells have pale outlines, in the middle the elongated nucellar cells are seen, and at the top (high focus) the aleurone cells have dark outlines. × 400.

PLATE 2

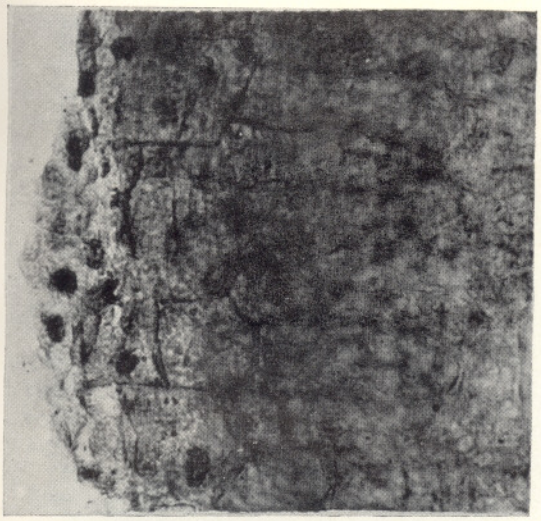
6. *C. nathorsti*, micropylar region, showing tissue of the "micropylar collar" above the nucellus. × 200.

7. *C. sewardi*, partly macerated stone cells dissected off as a coherent sheet and fixed with calcium chloride. × 400.

8. *C. sewardi*. Nucellus surrounded by inner epidermis of integument, whole cell walls preserved. A few cells on the left have shrunk into oval sacs. × 100.

9. *C. nathorsti*. Base of seed showing tissue of "chalazal plug" extending to the hilum. × 100.

10. *C. sewardi*, base of seed showing chalaza and delicate cuticle of integument. The aleurone cells have formed transverse plates. × 100.



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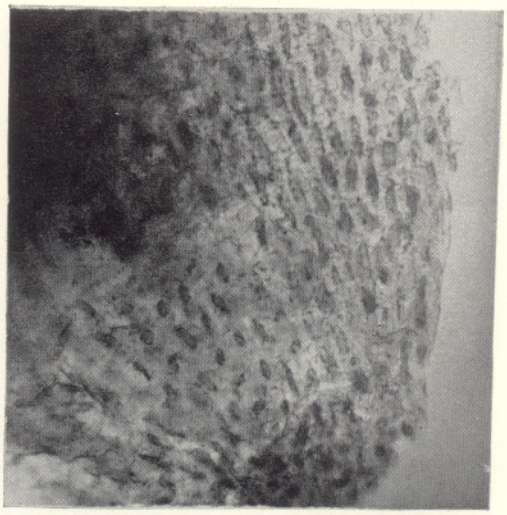

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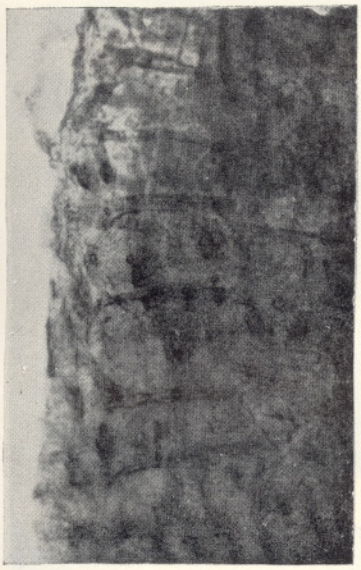

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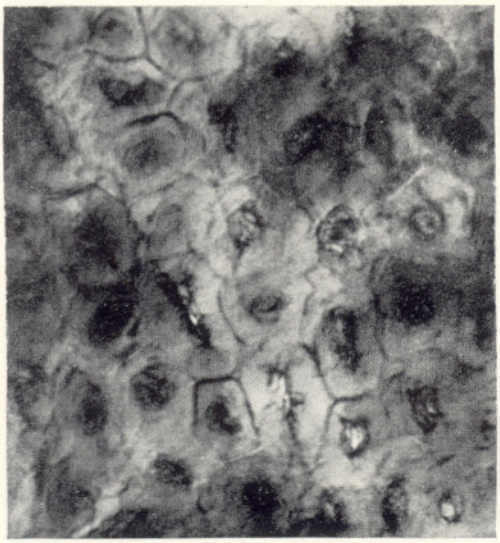

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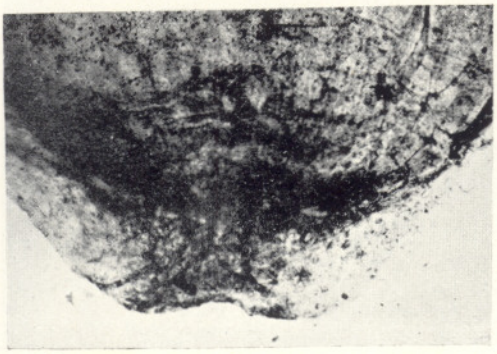

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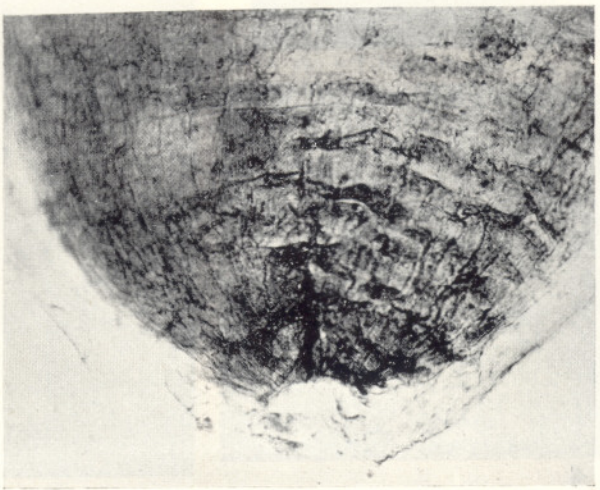

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