VI. *The Caytoniales, a New Group of Angiospermous Plants from the Jurassic Rocks of Yorkshire.*

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(Received June 20, 1924,—Read Feb. 5, 1925.)

[Plates 11–15.]

Contents.

Introduction.

The study of fossil plants during the last quarter of a century has revealed a vast amount of information about the past history of many modern plant types. But while we have learned much about the Pteridophyta and Gymnosperms, singularly little information has been gained about the evolution of the plants now dominant in the vegetation of the world—the Angiosperms.

In 1879 Darwin wrote the well-known lines to Hooker* :—" The rapid development, so far as we can judge, of all the higher plants within recent geological times is an abominable mystery. . . . I should like to see the whole problem solved."

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* Charles Darwin, ' More Letters ' (1903), p. 20.

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Though 45 years have passed since this was written, we are still hopelessly in the dark about the origin and early evolution of this, one of the largest classes of living organisms. Interesting theories have been put forward as to the possible origin of the angiosperms, but these have been almost entirely unsupported by fossil evidence.

We have a considerable mass of information about the angiosperms of Quaternary, Tertiary and Upper Cretaceous times, among which we find many forms closely similar to recent genera, but we know little of their history in the previous epochs. Two significant discoveries have, however, been made, which seem to indicate the presence of an angiospermous element in the vegetation of Jurassic times.

Dr. MARIE STOPES has found petrified fragments of angiosperm wood of diversified types in the Lower Greensand beds of England,* which points to the passage of this group through a previous evolutionary period of considerable extent. In 1904 Prof. SEWARD described a leaf from the Stonesfield slate, of Middle Jurassic age, which seems to be undoubtedly dicotyledonous in character.† But apart from these indications, we have previously had no certain knowledge of the occurrence of angiosperms in Jurassic times nor any idea of the nature or affinities of the earliest representatives of this group.

The present communication records the discovery of fruits, seeds and groups of stamens, which have a strong claim to be regarded as parts of angiospermous plants, in the Middle Estuarine beds of the Jurassic series of rocks of the Yorkshire coast. This find suggests not only that one group of angiosperms was common throughout the world at this period, but also that this group of plants may be traced back to Triassic times, and that it may have originated at the same time and in the same area as the bulk of the Mesozoic flora, of whose origin we, as yet, know little.

In this work not only the external features have been investigated, but also some of the internal structure. By the elaboration of a new technique some information has been gained about the structure of the seeds and fruits. These archaic plants have been placed in a class named the Caytoniales.

Throughout this paper the term angiosperm is used in its literal sense, as implying a plant with a closed carpellary structure enclosing ovules, and possessing a stigma, later giving rise to a true fruit. In the current usage of this term, we frequently imply far more, and mean plants with a certain type of stem and leaf structure which possess flowers. Here, however, the groups of reproductive structures differ greatly from the flowers of modern plants, but the structure of the carpels and fruits is such as to justify the use of the term angiosperm in its literal significance.

The first specimens of this group were discovered in April, 1911, and were mentioned in a communication‡ made to the British Association, Section K, at the Portsmouth meeting in that year. Shortly after their discovery I had the opportunity of showing

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* STOPES (1912).

† SEWARD (1904), p. 152, Pl. 11, figs. 5, 6.

‡ THOMAS (1912), p. 569.

them to Prof. NATHORST in Stockholm, who regarded them as belonging to a completely new and novel type. During the succeeding years efforts were made to collect further examples before commencing a detailed study, and eventually the present collection was amassed, the male organs being only obtained in 1922. After the interruption of work caused by the War, I devoted a considerable amount of time to working out new methods of study, and after much fruitless labour, the technique described in this paper was evolved. This, however, is still far from perfect and very many of the sections cut are wasted. Some further account of the progress of the work was given at the Edinburgh meeting of the British Association in 1921.*

At the present time I do not regard the investigation as complete, as I have not yet been able to prepare sections of the fruits of *Gristhorpia* showing structure. Owing to the length of time taken by the processes and the uncertainty of obtaining successful results in the end, it has seemed unwise to postpone further the publication of the results already obtained, which are of interest to a wide field of biologists. It is hoped that the results set forth below will give a sufficiently complete account of these novel plants to be of use to systematists, and that they may also attract the attention of some chemists who may be able to assist in the perfection of the technique.

THE MATERIAL.

The material collected for the study of these plants consists of about 160 specimens, showing the remains of fruits, seeds or anthers lying on the surface of pieces of grey shale. In most cases several separated fruits are seen in each specimen, often with a number of isolated seeds. I have also many fruits which I detached from the rock at the time of collection in order to facilitate transport, though in this process the fruit stalk is usually broken off. Almost all the material shows a very good state of preservation. The outer skin of the fruits was well cutinised and there are no signs of decay before preservation, though some of the burst fruits of *Gristhorpia* seem to have undergone some change. In almost all cases the fruits and seeds are considerably flattened and their stalks are often compressed, but some of the seeds of *Caytonia* have undergone so little deformation that the outlines of the outermost cells of the testa can be made out under the microscope. All the plant substance has been converted into a brittle coaly material which is opaque, but exhibits a brown or yellow translucence in sections about 5μ in thickness. In many cases the fruits appear to have contracted considerably and show a system of irregular wrinkles on their surface, being very comparable in their appearance to small hard currants. The microsporophylls are also well preserved, but the anthers are often split longitudinally, either owing to pressure or to previous dehiscence.

The microsporophylls were found several yards away from the spot where most of the fruits and seeds were obtained, and the fruits of the two genera are generally found apart, but occasionally both genera are represented in the same hand-specimen.

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* THOMAS (1922), p. 452.

THE LOCALITY.

Most of the specimens were obtained from a small area at the south end of Cayton Bay, on the coast of Yorkshire, between Scarborough and Filey. Here, on the beach, is found an outcrop of the famous Gristhorpe bed, which in former years was carefully studied by PHILLIPS, WILLIAMSON, LECKENBY, and others in exposures in Gristhorpe Bay about 500 yards to the south of my main locality.

The bed containing these plants is a fine grey shale, which is full of plant remains in a most perfect state of preservation. It belongs to the Middle Estuarine series, and is one of a series of beds of shale and sandstones lying between the Millepore Oolite and the Scarborough Grey Limestone, of Bajocian Age, in the Middle Jurassic series. The section at the spot is as follows :—

Massive sandstone with vertical roots	3 ft.
Black micaceous shale with *Equisetites*	6 ft.
Grey laminated sandy shale with roots	12–18 in.
Dark grey sandy shale with narrow black bands	6–8 in.
Massive grey laminated sandy shale with current bedding	4 ft.
Black shale	2 in.
Hard massive sandstone	1 ft.
Sandstone with grey streaks and remains of wood	4 in.
Grey sandy shale with remains of wood and some plants	9 in.
Fine grey shale with many plants (Gristhorpe Plant bed)	2 ft. 6 in.
Black shale with much wood and fragmentary plants	1 ft. 6 in.
Massive sandstone with black laminations and roots in upper part	5 ft.

The outcrop of the plant bed is seen at the base of the cliff forming Gristhorpe Point, but on turning the corner into Cayton Bay it descends on to the beach and soon runs into the sea. The best specimen of fruits and seeds was obtained at a point where the bed is covered normally with sand and shingle, and is near to the spot where *Williamsoniella* was obtained. The male flowers—*Antholithus Arberi*—were obtained at a spot where the bed is exposed between tide-marks. Some specimens have been obtained from the same bed in Gristhorpe Bay, near the Point, but here the fruits are not so numerous. Isolated seeds have also been noticed in the black coaly shale below the Gristhorpe bed, at one or two spots between Cayton and Gristhorpe Bays.

TECHNIQUE.

The material collected has been examined in its naturally occurring state, a binocular microscope being of great assistance. It is often possible to clear up the finer detail by brushing away the matrix with a fine brush wetted with water. Selected fruits have also been detached from the matrix and softened by boiling for a considerable time in a saturated alcoholic solution of caustic potash, when they swell somewhat and approach to a slight extent their original appearance.

On other specimens the maceration method has been used with very good effect. The usual solution of potassium chlorate in strong nitric acid is followed by aqueous alkaline solution, either ammonia, potash, or ammonium carbonate being employed as alkalies. This method has been very valuable because it not only renders visible the external cuticles, but also fibres and certain internal cutinised membranes, such as the megaspore membrane and the micropylar canal of the seeds.

In addition to these well-known methods, I have for this work used a technique which is, I believe, a novel one, and which appears to have great possibilities for palæobotanical work. It has not been yet satisfactorily developed to its full extent, and the successful preparations are accompanied by a great many failures, but the results achieved are of importance, as may be readily seen by inspection of the photographs on Pl. 13, figs. 28–32.

I do not propose to describe the method fully here, but the main features of the process are as follows:—Specimens are boiled for three to five weeks in saturated alcoholic potash, when they swell and become softened. They are desilicified in hydrofluoric acid, which mainly is of use for removing the adhering particles of matrix. They are then passed through alcohols, the material becoming harder again, and finally imbedded in celloidin. Thin sections are then cut with a microtome. These sections, if sufficiently thin, are brown and translucent in appearance, completely solid, and almost homogeneous. They show no structure save that of the thicker cutinised walls (*cf.* Pl. 12, fig. 18). The structure of the sections is then developed up by chemical treatment.

Several methods have been employed for this purpose. The principle underlying their use is, that the material forming the sections, though apparently almost homogeneous in structure, is composed of the compressed remains of the original cell structure, and that the various parts of the cells were and are heterogeneous in chemical composition. The middle lamellæ in particular were different from the substance which composed the rest of the cell walls. If by the use of chemical reagents it is possible partially to dissolve away some of the constituents, while leaving others more or less intact, the cell structure may become visible, in the same way that the crystalline structure of metals may be rendered visible by etching. Since, also, we find from maceration in bulk that the fruits contain a number of cutinised membranes, it may be possible by further solution to obtain information on the positions and nature of these membranes.

In practice the above idea can be realised to some extent, but it is rendered very difficult owing to the brittle and fragile nature of sections which are only 5–10μ in thickness, and which expand or contract in the various solutions. By treating sections with a solution of potassium chlorate in strong nitric acid they become light yellow in colour. On washing and transferring to a warm mixture of alcohol and formalin, the middle lamella of many of the cells either dissolves out or becomes visible (*cf.* Pl. 13, fig. 25). If instead of formalin a very dilute solution of ammonia in alcohol is used, the solution of the cell substance proceeds in a different way, the whole becoming more or less transparent; when the solution is stopped at the right moment, a good deal of the structure may be seen. By longer treatment little but the cutinised membranes are left (*cf.* Pl. 13, fig. 31), and a similar result may sometimes be obtained by oxidation of the sections with chromic acid. Another method which has given some good results, but which is associated with great manipulative difficulties, is first to treat the sections with a solution of potassium chlorate in strong hydrochloric acid, and then, after washing, to boil gently in very dilute sodium sulphite which has been rendered faintly alkaline. In all cases the contrasts can be accentuated by staining and the preparations are subsequently mounted in glycerine or balsam. These processes would be greatly facilitated if some transparent cement could be found by which the sections might be attached firmly to glass, during at least a part of their treatment, but up to the present no such cement has been discovered.

It is hoped that further research on these methods will bring them to a greater state of perfection, when they will probably be applicable to a great number of other cases in which plant remains are found in a coaly condition, and also to the study of coal itself.

Description of the Fruits and Seeds.

The specimens to be described fall into four groups—two groups of carpels, fruits and seeds; one group of microsporophylls with anthers, and finally the leaves associated with the above remains. All these are regarded as having been derived from one group of plants to which I have given the name of the *Caytoniales* and probably may be included in one family the *Caytoniaceæ*. For reasons given below I separate the megasporophylls, carpels and seeds into two genera, *Gristhorpia* represented by the species *Gristhorpia Nathorsti*, and *Caytonia* represented by the species *Caytonia Sewardi*. The male sporophylls probably belonged to the plant which bore the fruits and seeds termed *Gristhorpia*, but it is not certain that they did not also come from the *Caytonia* plants, so it seems safer to keep them, for the present, in a separate genus. Some similar specimens have been already described by Prof. Seward as *Antholithus sp.*, so I propose to give them a specific name and to call them *Antholithus Arberi*. The associated leaves will be described under their well-known name of *Sagenopteris Phillipsi* (Brongn.).

The two new generic names are derived from the locality. The specific names are proposed as a mark of respect for the three well-known Palæobotanists, to whose encouragement and assistance I owe much.

(*a*) *Gristhorpia* gen. nov.

Diagnosis.—Infructescences or megasporophylls, with stalk showing dorsiventral epidermal structure, bearing sub-opposite carpels or fruits in two rows. Carpels and fruits on short pedicels, spherical or pyriform, enclosing numerous ovules or seeds. Stigma a conspicuous broad lip or flange, with a recurved outer margin, produced at the basal end of the carpel adjoining the pedicel. Ovules distributed irregularly over a large part of the innerside of the carpel wall. Fruits fleshy when mature, often showing a radial rupture near the apex. Outer epidermal cells of fruits strongly cutinised with straight walls. Seeds small, elliptical. Testa with smooth external surface, without fibres or strongly indurated cells. Micropyle lined with elongated or rectangular cells.

Gristhorpia Nathorsti sp. nov. Pl. 11, figs. 1–13. Pl. 14, figs. 41–42. Pl. 15, figs. 43–47.

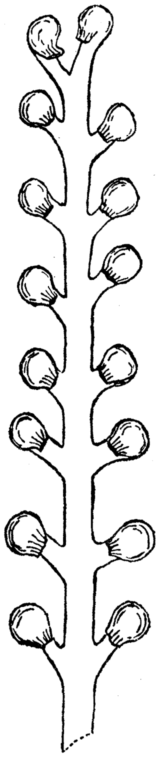
The Infructescence.

Several specimens have been found which show a central stalk bearing on either side short branches terminated by the remains of more or less spherical structures which were either fruits or carpels. These infructescences (or inflorescences) are all incomplete, no specimen showing both base and apex, nor indeed have the basal and apical ends been clearly recognised. The central stalk or axis was probably at least 5 cms. long when mature; the longest specimen shows a group of fruits about 4 cms. long, apparently incomplete at both ends, though the actual axis is only seen in the basal portion. A young specimen (G. 1) is about 3 cms. long, and in this distance probably bore eight pairs of carpels. (Pl. 11, fig. 4.)

The axes are between one and two millimetres broad, sometimes quite smooth and flat, but often showing irregular longitudinal wrinkling as would be produced by the squashing or contraction of a soft tissue. The wrinkling is usually seen when the structure has been compressed laterally, and it is very unlikely that the axis was woody.

The fruits and carpels were borne on short pedicels which seem to have been arranged in a sub-opposite manner in two lateral rows on the axis (text-fig. 1). Few of the more complete specimens show this clearly either owing to lateral compression, or to the way in which the specimen lies with reference to the plane of cleavage of the matrix. In G. 1, for instance, the axis appears to have carpels on one side only, but there are indications of a second row in the matrix below the series seen on the surface. In some specimens, however, most of the fruits seem to lie in two rows, one on either side of the axis (*cf.* G. 20, Pl. 11., fig. 5). Several smaller fragments show the same feature.

The fruits and pedicels appear to have been detached from the axis when ripe, leaving an elliptical scar (Pl. 11, fig. 1), and several specimens show a two ranked arrangement of these scars. Some of these old axes can be detached from the matrix and the scars are then found to be in pairs on opposite sides of the axis.



TEXT-FIG. 1.—*Gristhorpia Nathorsti.* Restoration of a young megasporophyll showing the arrangement of the carpels. ×2.

Thus, it is fairly certain that the carpels, if they can be so termed, were arranged on the stalk in a pinnate fashion. It is not certain whether the carpels of both sides lay in the same plane as the axis. The existence of several specimens in which the carpels of the two sides are compressed one on the other seems to indicate that the reverse was the case. Cuticle preparations of the axis also seem to support this idea.

The pedicels have a length of 1 ·5 to 3 mm. and are about three-quarters of a millimetre broad at the point of insertion on the axis, enlarging somewhat as they pass up to the base of the fruit. They showed little growth in length as the fruit matured, the youngest being over a millimetre long, while the oldest seldom exceed 3 mm. in length. (Pl. 11, figs. 1, 6, 7.)

The cuticular structure of the axis shows some unexpected features. The cells composing the epidermis were not uniform in shape and cutinisation, those on one side differing from those on the other side; on both sides they are arranged in more or less longitudinal rows. The cells of the more thickened surface are somewhat rectangular in shape, their average dimensions being 22 ·5μ wide and 26μ long; the cells of the thinner side are more fusiform in shape and less regular, they average about 18μ wide and 37 ·5μ in length (Pl. 14, fig. 41). The differences in their shapes are shown in the figures on page 336 (text-fig. 11, A, B). There seems to be no sharp line of demarcation between the two surfaces. On the thinner side near the bases of the pedicels the cells are more or less isodiametric. (Pl. 15, fig. 45.)

When we consider the shape of the inflorescence-like structure, with the fruits arranged sub-oppositely in two rows like the pinnæ on a leaf, and, in addition to this, find that the cuticle of the central axis shows a marked dorsiventral structure, while there is no trace of bracts or bract scars, we have strong grounds for regarding the whole structure as foliar in nature. My first impression was that we had a racemose inflorescence on which the carpels were arranged in a spiral fashion, and in the preliminary description given to the British Association, Section K, at Edinburgh in 1921, I described them as such. On further careful extraction of the stalks from the matrix, and renewed examination, I have come to the conclusion that we cannot regard these structures as cauline in nature, and that we are not dealing with either a racemose or a cymose inflorescence, but with a compound megasporophyll. The so-called carpels are not then formed by the laminæ of entire sporophylls closing round the ovules, but from the laminæ of pinnæ only. It is very doubtful whether the term carpel should be applied to such structures, but this word seems to have been used to cover such a wide morphological range of structures that it may be permissible to use it here. The terms pistil and ovary do not seem suitable, and it would seem desirable to have a term of more limited application which would stress the special feature of the angiospermous gynæceum, viz., the closed ovary formed by the carpellary structure.

Since, however, it is highly probable that the structures now to be described are strictly homologous with the organs generally called carpels in the angiosperms, I propose to use the term in this paper, having pointed out that in doing so

I mean a structure formed from a single pinna with its enclosed ovules, and not a structure formed from a complete megasporophyll.

The Carpels and Fruits.

The individual fruits were probably spherical or somewhat pear-shaped bodies measuring from 2–5 mm. across their transverse axis and slightly longer in a longitudinal direction through the stalk. When found they are generally crushed and are often less than 1 mm. in thickness and considerably wrinkled, but after prolonged boiling for several weeks in an alcoholic solution of caustic potash they swell somewhat, and probably begin to resemble their original condition (*cf.* text-figs. 2 and 3). It is then seen that the stalk is not inserted in the axial line of the fruit, but lies to one side, and close to the stalk the wall of the fruit tapers down to a lip-like structure, which is generally clearly seen, and forms the chief character by which the fruits of this genus can be at once distinguished. This lip is regarded as the stigma, and between it and the stalk was an opening of an inverted funnel shape which extended inwards towards the centre of the fruit. Apart from this structure and the system of irregular wrinkles, due, no doubt, to contraction, the exterior of the fruit possesses no further appendages and was formerly quite smooth. No traces of scars such as would be left by the falling-off of stamens or perianth can be distinguished on the fruits or on their pedicels.

I have been unable to find among recent plants any young fruit or carpel which closely resembles in shape that of *Gristhorpia.* Though one cannot safely apply any modern technical term in describing it, probably the fruit may be classed as a berry, as this has no implications with reference to the position of the stigma. The shape of the individual fruit can best be indicated by saying that its external form is closely analogous to that of an anatropous ovule, apart from the difference in size, the fruit stalk resembling the funicle in its position, and the stigma occupying the position in which the micropyle of the ovule would be seen.

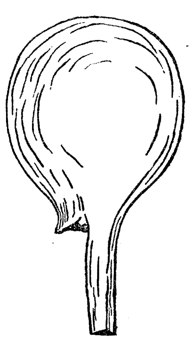
TEXT-FIG. 2.—*Gristhorpia Nathorsti.* Youngest carpel found. It indicates that the carpel wall may be formed by the overarching of the lamina. × 16. (*Cf.*, Pl. 15, figs. 46, 47.)

The youngest specimen found (*cf.* Pl. 15, figs. 46 and 47, text-fig. 2) consists of two fruits which seemed to have terminated an axis; they have a width of 1·75 and 1·5 mm. in the broadest part. In the larger example the fruit is yet but little broader than its pedicel which is rather more than 1 mm. thick, its stigma lies between the pedicel and the matrix, and is consequently scarcely visible. The right-hand fruit shows a very interesting form. The stigma is seen as a small projecting flap at the side, and the whole structure appears as though formed from a reduced foliar structure which was curved over at the apex, recurved and contracted to form a sac, and slightly expanded again to form the stigma at the tip, the peripheral outline being like that of a shepherd's crook. Though I have not risked the chemical treatment of this specimen for the microscopic study of its structure, it raises the crux of the whole question as to the nature of the *Gristhorpia* fruit. Was this the form of the carpel at the time of pollination and was the stigmatic cavity open or closed when pollination took place? In other words, was *Gristhorpia* a Gymnosperm or a true Angiosperm? There is little doubt that the ovary was closed when pollination took place, and if in this specimen the ovary was open at the time of preservation, it is only to be regarded as comparable with the carpels of several modern Angiosperms in early stages of their development.

The specimen G.1 shows a number of fruits which are also in a young state, but unfortunately here the stalks are all uppermost and the stigmas are not seen. Two of these fruits were detached from the matrix and treated with Schultz's macerating fluid, followed by ammonia, the cuticular membranes being thus rendered transparent for microscopic investigation. At this stage the whole of the outer wall of the fruit and stalk is distinctly cutinised, but not so strongly as in the older specimens; no traces of cutinised seed or megaspore membranes were detected inside the fruit (or carpel). The epidermal cells of the pedicel and of the part of the fruit above it (dorsal side) are more strongly cutinised than those of the curved over region or ventral side, showing already their irregular polygonal outlines. The epidermal cells in the neighbourhood of the micropyle are less cutinised and tend to be arranged in regular rows directed towards the lips of the opening. The latter was large in comparison with the diameter of the fruit, and was cutinised on the inside as well as on the out. This inner cutinisation extends up for a short distance and is then lost, or more probably the walls of both the inner sides met and closed the stigmatic opening. There is no indication of the carpel or fruit having originally been a hollow sac open to the exterior; on the contrary it is most unlikely that it had this form, for if so the fine mud of the enclosing sediment would have undoubtedly entered, and would have to some extent filled the cavity. Both the preparations made show that while there is some sediment in the stigmatic opening, the interior of the fruit is quite free from foreign matter.

In one of the preparations made from this specimen (Pl. 14, fig. 42) a further interesting point occurs. The fruit wall after clearing was broken up so that the cuticular membranes of the different parts were more or less separated and two small parts of the membrane covering the stigma were detached. On examining these under the high power the cuticle seems to be very thin and the outlines of the isodiametric original cells are only very faintly visible. Attached to this thin membrane the coats of nine or ten microspores are seen and these have a very distinct form. They appear to consist of a central cell, in one case apparently ruptured on one side, accompanied by two more or less spherical sacs, one on either side. Their walls were covered with minute granules. These microspores have thus a very characteristic shape, and one or two further examples are seen in a second preparation from a carpel or small fruit. They have been traced to their source and will be described later in the section dealing with male flowers. In addition one preparation shows two much larger spores lying close together. They are darker, of a different shape, and may be regarded as the remains of microspores of some other plant.

Passing on to consider the larger fruits such as G.2 (Pl. 11, fig. 1, *cf.* text-fig. 3) we may notice that the fruit became about 4 mm. broad, and was probably softer as well as larger. Conspicuous longitudinal wrinkling is seen, which runs down to the stigmatic flap, but stops short at a distance of about 1 mm. from the stigmatic opening. Evidently the body of the fruit had swelled more than the stigmatic part, which is left as an almost smooth flap near the stalk.



TEXT-FIG. 3.—*Gristhorpia Nathorsti.* Drawing of a young fruit from a soaked specimen. Note the stigma at the base. × 8.

In another specimen (Pl. 11, fig. 3) the stigmatic flap is seen a little to one side of the fruit; it is here much less obvious and seems to have been constricted. As might be expected, the stigmatic structure becomes less obvious as the fruit increases in size, and in the older specimens it cannot be distinguished without careful examination after the removal of the adhering sediment. Most of the older fruits (diameter more than 4 mm.) are no longer intact, but appear to have been burst open by an irregular but more or less apical fissure of the fruit walls. In the fissure or just outside it seeds or other small bodies are often seen (Pl. 11, figs. 8, 9). It is not possible to ascertain with any certainty whether these specimens, which are almost always detached from the peduncles, show the natural mode of dehiscence of the fruits, but the evidence seems to point strongly to this rupture of the fruit wall having been caused by the weight of the superposed sediments before the matrix had become consolidated or the fruit dry. These ruptured fruits seldom contain much of the muddy matrix which should have filled them if they were open at the time when they were buried, and it would be difficult to account for the presence of seeds in the fissure except on the view of rupture *in situ* by pressure. If this is the case it seems to indicate that the fruits had a somewhat fleshy nature with a thin outer wall, and were, in fact, berries.

From some of the ruptured fruits the contents, consisting of a number (8–10) of more or less mature seeds and a large quantity of small rounded bodies, had been extruded. These latter are of somewhat varied shape, being generally ovate or pear-shaped, but occasionally more or less spherical. They are from 0·1 to 0·3 mm. long and about 0·08 to 0·1 mm. broad (Pl. 15, fig. 43). By Mr. Walton's method* I attempted to separate some of those bodies from the matrix, but they tended to break up a good deal in the process and their shapes appear much less regular than when seen *in situ.* In the preparation obtained a number of more or less club-shaped or pointed bodies were also seen (Pl. 15, fig. 44).

In one or two specimens (especially in S.S.1) the wall of the fruit appears brown and membranous and a certain amount of sediment had reached the centre of the fruit, possibly owing to some decay before preservation. In one of these it was possible to remove part of one wall of the fruit and to see a portion of the interior. Here we find

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* WALTON (1923).

a very large number of small, rounded bodies, of a shape and size similar to those apparently expressed from the fruits mentioned above. They show little or no regularity in arrangement, but, presumably, were originally attached to the fruit wall.

What is the nature and origin of these bodies? On treating some of them with SCHULTZ's solution and ammonia they dissolve almost entirely, showing no trace of cellular structure or cutinised membranes. It seems not unreasonable to suppose that most of them, if not all, were formed from the remains of ovules which failed to develop. They are, however, very small and, if really ovules, had not reached the stage in which a distinct megaspore membrane was formed. They may be the remains of hard groups of stone cells imbedded in the wall, but in this case it is strange that they should be so readily extruded from the fruits with the seeds, or they may be internal vegetative structures. If they do represent aborted ovules, two points are apparent, viz., that the carpels contained a very large number of ovules, and, secondly, that these possessed parietal placentation.

Examination of the Fruit by Maceration.

When an entire fruit is treated with SCHULTZ's macerating solution for some hours and afterwards transferred to dilute ammonia, the material composing it is for the most part dissolved away, and only certain cell membranes remain, which are generally regarded as more or less cutinised. The outer membrane of the epidermis is left as a fairly thick and tough structure, while within are a number of much more delicate membranes derived from the seeds (Pl. 11, figs. 2, 3).

The epidermal membranes show fairly clearly the shapes of the epidermal cells. In the pedicel the cells are small and seem to be arranged in regular longitudinal rows on the dorsal side, while they show no such arrangement on the ventral side. Where the pedicel passes into the fruit the cells become somewhat larger, and on the dorsal side (away from the stigma) the same longitudinal rows can be traced but become much less regular. Here the cells are very irregularly polygonal, the longitudinal walls which run up towards the apex of the fruit being more strongly thickened and more regularly arranged than the transverse walls, as in the main stalk. On the other side of the fruit, as we approach the stigma, no regularity of arrangement can be traced, and the thickening of the polygonal or rounded cells is fairly uniform. In the stigmatic flap the arrangement in longitudinal rows becomes once more very pronounced.

Preparations of the stigma show the flaps covered on both the inside and the outside by cutinised cells of approximately isodiametric rounded form, arranged in regular vertical series. Sometimes these cells form small papillæ at the surface. Towards the centre of the fruit the preparation becomes thicker and almost opaque in certain vertical bands, due to the increase both of the individual cells and of the number of cutinised cells in the tissue as shown by sections. Adjoining this region a more delicate membrane is seen, composed of elongated cells with characteristic rounded ends. The membrane ends irregularly due to the fact that it becomes increasingly thinner as the centre of the fruit is approached and that it has been torn in the making of the preparation. Some light is thrown on the nature of these stigmatic membranes in the next section.

The form of all these cells in the epidermal membrane is characteristic and differs from that seen in *Caytonia*.

The membranes derived from the seeds are generally fragmentary (Pl. 11, figs. 2, 13) as they are very delicate, and break up when the fruit is opened to extract the seeds. They are of two types: (*a*) the remains of the slightly cutinised seed coats and parts of micropyles; (*b*) the remains of a characteristic thicker membrane which is regarded as the megaspore membrane. These will be described later, as they are more clearly seen when isolated seeds are macerated. It should be observed that the extraction of these seed membranes is definite proof that seeds were produced inside the *Gristhorpia* fruit, and that the characteristic shape of the membrane cells, especially in the micropylar region, enables us to assign with confidence certain isolated seeds to their original fruit genus.

Structure of the Fruit.

Little is yet known as to the structure of the fruit of *Gristhorpia*. The methods which were devised for the investigation of the fruit of *Caytonia* were employed on some specimens of *Gristhorpia*, but gave no useful result. Probably the seeds in this genus were not so woody or fibrous, or the condition of the material was not quite the same. It is hoped that later investigations will result in new methods being discovered which may reveal the cellular structure of these fruits, but there is no immediate prospect of this result being obtained.

A few points of structure can be ascertained by cutting thin sections of fruits in a longitudinal direction, passing through the micropyle, by the methods already described. The fruit shown in text-fig. 3 was cut into a series of sections each about 7μ thick. They were very brittle and broke into many fragments, but without further treatment showed the relations of the more strongly cutinised parts. The cuticle of the epidermis of the fruit was of considerable thickness and the stigma was also strongly cutinised. This alteration is not confined to external walls, but also extends into the interior where we get strands of cutinised tissue surrounded by brown material.

The vertical section through the stigma shown in Pl. 11, fig. 10, is like a section through a funnel. The structures described above as the stigmatic flaps are seen to bound a conical opening, nearly half a millimetre long, with its apex toward the interior. The sides of this opening were lined with cutinised cells which were often papillate; at the apex there is a solid plug of completely cutinised cells about 70μ thick and composed originally of about 12 to 14 cells. As we pass toward the centre of the fruit this plug becomes divided into two parts by a line of the same structureless material which composes the whole of the interior, and which represents compressed, cellular material. This line gradually widens and the cutinised cells thin out and disappear. The remainder of the fruit shows no trace of structure.

Though there is little on which to reconstruct the original structure of the stigma, it seems clear that it had originally a funnel-shaped opening in the centre, surrounded by papillate cells upon which the pollen grains became lodged, and that this opening narrowed and became closed by continuous tissue. Probably in the young state the neighbouring cells were rich in sugars or other substances, which were secreted and made the stigma sticky. Later the presence of such substances was, perhaps, responsible for the heavy cutinisation, not only of the superficial cells, but also of those in the adjacent tissue, extending into the body of the fruit. These cells have retained their individuality, while all the rest have been compressed into a homogeneous mass.

Such a process of cutinisation in cells which were previously rich in sugars is not without parallel in recent plants. It seems to be a regular feature in the micropyles of Gnetalean seeds, and is especially seen in *Gnetum gnemon** and *G. scandens*.†

The Seeds.

Little can be discovered about the structure of the seeds from the examination of the fruits in this genus, though by careful extraction of the megaspore membranes from macerated specimens it would appear that 10–12 seeds usually matured within each fruit. We find, however, many isolated seeds lying in the matrix (Pl. 11, fig. 8), often in close proximity to squashed open fruits, which show us their external and some of their internal characters. They are small elliptical bodies, much flattened, and very even in size. The lengths of their axes are approximately 2 mm. and 1 mm. (Pl. 15, fig. 43). When extracted from the matrix they are 0·3 to 0·5 mm. thick. They are opaque, black, and brittle; externally they are quite smooth. Their flattened shape may be entirely due to compression, but, on the other hand, they show no irregular wrinkling such as would probably be produced during the compression of an ellipsoidal structure. They are sometimes slightly less curved at one end, and here a trace of an attachment scar may rarely be made out. The micropyle is at the other end, so that they were orthotropous. They are similar to the seeds of *Caytonia*, but may be distinguished by their smooth exterior, their greater thinness, and their somewhat more elongated shape. When these seeds are placed in SCHULTZ's macerating fluid and afterwards in a dilute solution of ammonia or caustic potash, the usual clearing action takes place and a certain amount of their internal structure is revealed (Pl. 11, fig. 12). A 10 per cent. solution of ammonium carbonate is also useful as a clearing agent, and the processes of the reaction are somewhat different when it is used. The outer integument becomes ruptured and broken up, the solution of some of the middle lamellæ of the cells taking place before the clearing of the cell walls themselves. The most satisfactory reagent is a 1 per cent. solution of caustic potash, which brings about a slow, regular solution of the brown (humic) material without the rupture of any of the membranes. When the clearing process is complete, nothing remains of the seed except two fine

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* THODAY (1921), p. 38.

† THODAY (1911), p. 1119.

membranes; an inner, thicker membrane, which is probably to be regarded as the megaspore membrane; and the outer, much thinner membrane, which is the cutinised outer wall of the testa.

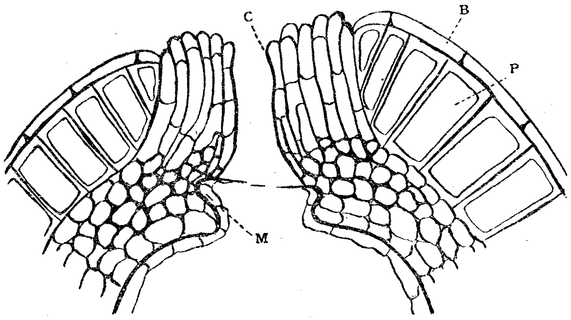
At one end the two membranes are joined by a tubular structure, the cutinised walls of the micropyle, while at the chalazal end connecting tissue has completely disappeared.

The testa wall membrane is very thin, and is generally broken in washing and mounting. It seldom shows any traces of its original cell outlines except near the micropyle. In some specimens, however (cleared with ammonium carbonate), faint indications of hexagonal or elongated rectangular cell-outlines are seen, in which the walls are characterised by the possession of fine projecting points. The megaspore membrane has a strong brown colour, probably indicating the existence of a good deal of cutinisation. The membranes from both sides of the seed are intimately pressed together, but show the outlines of the cells which lined them. In some cases, where the clearing has not been carried too far, there is a suggestion that the entire cells lining the megaspore membrane may have been somewhat thickened. They seem to have possessed a fairly regular, elongated shape. They are less elongated towards the micropylar end, and sometimes the walls show fine sinuous folds, which may be artificial and produced as a result of the chemical treatment. At the basal end the cells usually appear as though broken off, but sometimes the membrane is elongated into a distinct point which almost touches the testal membrane at the point where the seed was originally attached.

The megaspore membrane has a characteristic appearance at the micropylar end (Pl. 11, fig. 11). Its cells appear smaller, isodiametric, and show a considerable amount of thickening at or near the point where they abut on the micropylar tube. These thickened cells form a sort of flange or neck, which is rather broader and quite distinct from the delicate cell membranes lining the micropylar tube (*cf.* Pl. 11, fig. 11). It may, perhaps, be suggested that in this neck or plinth we have the remains of a small pollen chamber once lined by sugar-secreting cells, and later cutinised, but no proof of this suggestion is available. The micropyle of these seeds is always clearly seen in carefully prepared specimens as a fine membranous tube derived from the walls of the cells which originally lined the orifice in the integument. It is about 0·08 mm. wide, and appears as if composed of small, elongated, fusiform cells. These cells are quite distinct from those of the megaspore membrane on which they abut below. They differ in shape from the corresponding cells in *Caytonia.* They extended to the outside of the testa, where the cells immediately surrounding the micropyle were also cutinised strongly on their outer surfaces. This micropylar cutinisation formed a little apical flange round the orifice. In good specimens there is a distinct groove bounding it from the testa cuticle, and while in some cases it forms an elevation, in others it lies in a small depression below the surrounding testa (*cf.* text-fig. 4). Its appearance suggests that there may have been two integuments.

We have no examples of the present genus which show their internal structure as in

Caytonia (*cf* .p. 23), but from the fortunate preparation shown in Pl. 11, figs. 11 and 12, some points can be made out. In this case solution was carried out very slowly in dilute caustic potash and the cuticular structures described above are clearly seen. The cell outlines in most of the apical tissue are visible; those immediately surrounding the micropylar tube, being very thin and elongated, differ from the surface cells of the outer integument which present rounded or hexagonal outlines. In addition, the remains of another zone of cells are seen in the neighbourhood of the micropyle; they are the faint brown membranes of a tissue which appears to have surrounded the micropyle and then extended outward and downwards round the megaspore membrane in a way suggesting a second integumental covering. At first they are distinct and rounded, but as they pass down over what one may term the shoulder of the seed they become thinner and more elongated, soon disappearing. Possibly, however, these cells may correspond with the fibrous layer of the outer integument of *Caytonia* and not to an inner integument.



TEXT-FIG. 4.—*Gristhorpia Nathorsti.* Apical part of a seed reconstructed from information furnished by macerated specimens. × 100. B. Blow-off layer. P. Palisade layer. C. Cutinised cells lining the micropyle. M. Apical enlargement of the megaspore membrane comparable to the Pteridosperm plinth.

Thus the seeds of *Gristhorpia* were complex structures of characteristic form. It is impossible to determine whether they contained a resting embryo at the time of preservation, though we can be certain that the membranes, here regarded as the megaspore membranes, contained a considerable amount of carbonaceous material. The integumentary structure was not so woody or stony as in *Caytonia*, but comparison of macerated specimens leads to the belief that *Gristhorpia* possessed a palisade layer and a "blow-off" layer as in that genus (see text-fig. 4).

(*b*) *Caytonia* gen. nov.

Diagnosis.—Carpels sub-opposite, borne in two rows on central stalk (megasporophyll) with dorsiventral epidermal structure. Carpels and fruits spherical, with short pedicels. Stigma, a narrow semilunar flange in close contact with the pedicel. Walls of fruit thin when mature, outlines of contained seeds visible. Epidermal cells of fruit with sinuous walls. Orthotropous ovules in two rows on dorsal wall of ovary. Seeds small, elliptical, with many minute pits on their outer surface. Testa complex, hard and woody. Outer integument of three layers. Inner integument forming micropylar tube and partly covering outer integument as a small flange at the apex. Cells lining micropyle rounded, isodiametric.

Caytonia Sewardi sp. nov. Pl. 12, figs. 14–24. Pl. 13, figs. 25–32. Pl. 15, fig. 48.

The second, and perhaps more important, genus is represented by infructescences, isolated fruits in considerable number and a large number of isolated seeds. Fruits and seeds have been studied by the maceration method, and microtome sections have been cut through mature fruits from which a certain amount of their internal structure has been observed. While there are strong resemblances in general form and structure to *Gristhorpia*, we find in this second group some very important differences which seem to necessitate its separation into a distinct genus whose name is derived from the locality where the first specimens were found.

The Infructescence.

As in *Gristhorpia*, the fruits were borne in opposite pairs on a slender central axis which was at least 4 cms. long, and approximately 1 mm. broad. This axis was produced on slender stems about 2–2·5 mm. broad. One specimen (Ca. 1), Pl. 12, fig. 16, shows the union of the axis with its small stem or twig, and is of considerable importance, for the surface of the axis below the lowest fruit is quite smooth, and shows no scars such as would have been present had the infructescence represented the gynæceum of a hermaphrodite flower with a perianth, or a strobilus. The arrangement of the carpels on the peduncle was probably similar to that of *Gristhorpia*; several specimens show fruits on their pedicels arising on opposite sides of the main stalk while in other cases they all appear to arise on the same side. In one specimen figured (Pl. 12, figs. 14, 15), the arrangement is not so clearly seen, as the peduncle lies beneath the fruits and is more or less embedded in the matrix. Where the fruits have disappeared pairs of scars are seen on the axis.

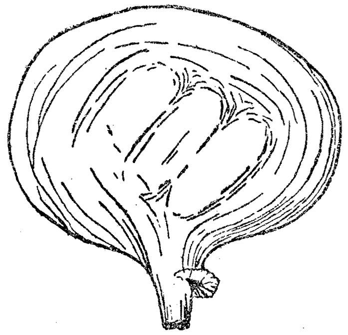
The cuticular preparations of the stalk bearing the carpels show indications of a dorsiventral structure. Preparations from the axis of Ca. 24 (text-fig. 12 A.B.) show this in a very marked way. The epidermis from one side of the peduncle was much more strongly cutinised and its cells were arranged in very regular longitudinal rows; the longitudinal walls were well thickened, showing a series of rounded or pointed projections, while the transverse walls were thinner and less regularly disposed. The cells of the other surface were less thickened, their walls have a more uniform appearance, they were thinner and less regularly arranged. No stomata are seen on either surface, but rounded papillæ or hair bases occur sparingly on both surfaces.

Here again we have to regard the carpels as representing the fertile pinnæ of a pinnate megasporophyll.

Fruits.

As in *Gristhorpia*, each fruit has a small but distinct pedicel about 2 mm. in length, but more slender than in the former genus and only about a third of a millimetre broad (Pl. 12, figs. 15, 16).

All the fruits which have been found are almost circular in outline measuring 2–4 ·5 mm. in diameter. None of them show the distinctly carpellary stage, as seen in *Gristhorpia*, but some differences in external appearance due to age may be noted. The smaller fruits have generally a smooth exterior surface. Those a little larger frequently show a complex of irregular wrinkles, probably due to contraction, while in some of the largest fruits the outlines of the contained seeds are clearly shown. It would appear that in the mature fruits the fruit wall was fairly soft and thin, while the seeds were very hard, consequently, on preservation and compression, they became clearly visible through the overlying wall (*cf.* Pl. 12, figs. 22, 23A).

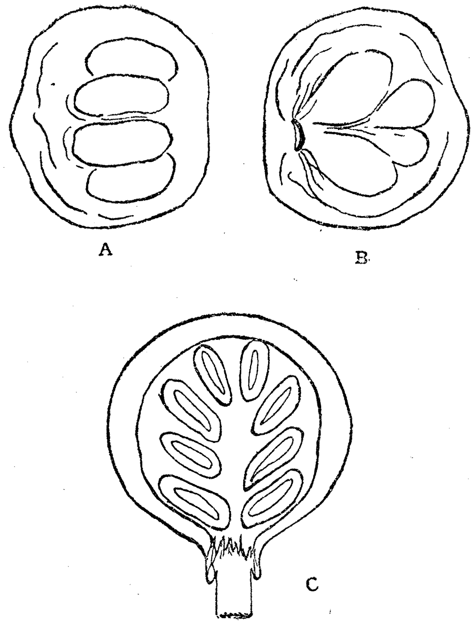

TEXT-FIG. 5.—*Caytonia Sewardi.* Fruit showing flange-like stigma on the stalk. × 7.

It is only in exceptional cases that the stigma can be seen. As shown by sections it formed a very small flange extending round one-half of the base of the fruit, adjoining the stalk. It is much less conspicuous than in *Gristhorpia*, but may be noticed in cases where an isolated fruit has been compressed longitudinally, or is lying in the matrix with the broken end of the stalk uppermost. It is a tiny flap not much more than half a millimetre across and possessing slight longitudinal striations (*s.* Pl. 12, fig. 17, text-fig. 5).

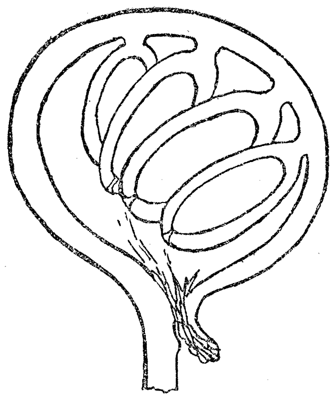
When the stigmatic region is obscured it is often difficult to distinguish between the fruits of *Gristhorpia* and *Caytonia* in isolated hand specimens. They may, however, be readily distinguished by the cuticle structure when macerated in SCHULTZ's solution, and subsequently treated with dilute ammonia. The epidermal cells in *Caytonia* are somewhat less strongly cutinised. They are small in size, varied in shape according to their position on the fruit, and are characterised by the numerous small pointed or rounded projections in their walls. These often give the radial walls a sinuous appearance or, extending over the surface walls, they produce an appearance of reticulations of smaller size than the actual cells. The thickening of these cells is somewhat similar to that shown by the epidermal cells of the axis.

The remains of 6–8 seeds can generally be extracted from the interior of a macerated fruit. These consist of megaspore membranes surrounded by fibres from the integument, also the remains of the micropyles, and very transparent fragments of cuticle from the outer integuments. In no case has any of the matrix been found inside a macerated fruit, and there seems to be no possible doubt that the carpel was completely closed at a very early stage in its development, if it were ever open. *Caytonia* then must have been truly angiospermous. The fruits did not burst open when compressed, in the same way as in *Gristhorpia*, and were perhaps less fleshy when mature, but two examples have been found in which part of the fruit wall (Pl. 12, fig. 24) has gone, disclosing some seeds inside. There is no evidence of the presence of unfertilised ovules.

We may gain some idea of the placentation and arrangement of the seeds by the examination of fruits which show the outlines of the contained seeds through their wall. In a number of cases these seeds are found to be lying in an orderly manner, which indicates that they were not detached from their funicles at the time of preservation (see text-fig. 6). In some cases the seeds lie in pairs, while where the fruit has been compressed with the peduncle below, the seeds seem to lie in a single row across the apical end of the fruit. Consideration of the various forms rules out the possibility of any central or axile placentation, and the most probable arrangement would be a double row of seeds (or ovules) extending up the wall of the fruit as far as the apex (*cf.* text-fig. 7). This agrees with the evidence obtained from sections.



TEXT-FIG. 6.—*Caytonia Sewardi* fruits. A. and B. Drawings of two fruits showing the positions of the included seeds. C. Diagrammatic section through a fruit showing an arrangement of seeds which on the compression of the fruit would give rise to the forms shown in A and B.



TEXT-FIG. 7.—*Caytonia Sewardi.* Diagrammatic section of a fruit to show the probable arrangement of the seeds and the stigma with its strands of cutinised cells extending into the inside of the fruit. × 7.

Isolated Seeds.

A considerable number of isolated seeds of this species have been found. They are elliptical in shape and very uniform in size, viz., 1·5 mm. long and 0·75 mm. broad (Pl. 12, fig. 21). They are, of course, much flattened, but may have been somewhat flat before preservation. They are at first sight very similar to the seeds of *Gristhorpia,* but may be distinguished owing to their being thicker—due to the original hard testa—and especially by their superficial appearance. The outside appears finely pitted;

some specimens show that the pits correspond to the lumina of the epidermal cells whose radial walls project to form a minute superficial network. Examination after chemical treatment seems to show that this superficial character can be relied on for the separation of the two genera.

As in *Gristhorpia,* maceration followed by immersion in an alkaline solution reveals some points of structure (Pl. 13, figs. 26, 27). The megaspore membrane and lining of the micropyle were strongly cutinised and become clearly visible after prolonged maceration. The cells lining the megaspore membrane are similar to those of *Gristhorpia,* being sometimes a little more elongated. There is, however, here no projecting neck at the apical end adjoining the micropyle, which was a fairly constant feature in *Gristhorpia.* Some slides give the appearance of a small depression in the megaspore membrane at the base of the micropyle tube, such as might have been left by a pollen chamber, but we cannot be sure that this is not an artifact.

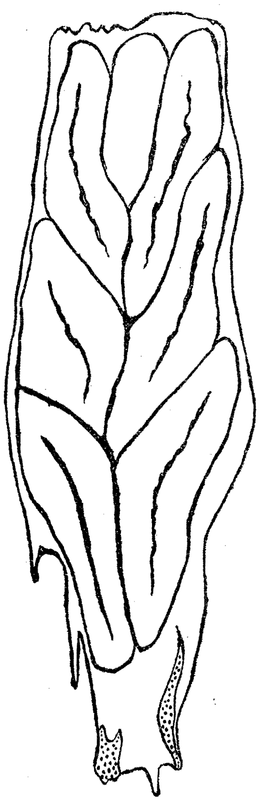
The remains of the micropyle in macerated seeds form a feature distinguishing them from the seeds of *Gristhorpia,* for the cutinised cells are different in shape and arrangement. Instead of being elongated they are rounded and isodiametric, and the micropyle forms a funnel-shaped opening, increasing in size from the megaspore to the exterior of the integument. The rounded cutinised cells spread out in a peltate form (*cf.* Pl. 13, fig. 26), and extend laterally over part of the apical end of the seed. They afford some evidence in favour of the view that the seed was originally a flattened structure.

When a seed which has been treated with SCHULTZ's solution is placed in a solution of ammonium carbonate and watched under the microscope, the usual brown "humic" substances commence to dissolve out, very soon, regular polygonal or hexagonal areas become visible, which are doubtless the palisade cells forming the outer part of the integument. These presently disappear, the material forming them being dissolved away, and next the spicular centres of a fibrous or stony layer are seen. This layer of fibrous cells extends completely round the seed from the micropyle to the base, and its macerated remains are shown in Pl. 13, fig. 27. The presence of this tissue is another character distinguishing these seeds from those of *Gristhorpia.* In a partly or fully macerated seed the fibrous layer surrounding the megaspore membrane is separated from the thin external cuticle of the integument by a space. When the external cuticle is examined it is found to show traces of elongated rectangular cells different in shape from the hexagonal cells which appeared during the early state of maceration. The nature of these elongated cells, which belonged to an original but evanescent cell layer, is elucidated by the sections cut through mature fruits.

The above description indicates that many interesting features can be made out from external inspection, and by the preparation of cuticles made in the method which has been applied already with much success by various workers. We may turn now to the consideration of the structure as revealed by my new technique of section cutting.

Structure of the Fruit and Seeds.

Sections showing structure have been obtained from three fruits, but owing to the imperfections in the technique, and to the large number of sections which broke up during the various processes to which they are subjected, I have not yet been able to obtain a complete series. The first set of preparations (Z) was made from a fruit which had been compressed in a direction at right angles to the stalk, and the contained seeds are found to be arranged in a regular manner, probably due to their position during life (text-fig. 8). The sections were cut in a longitudinal direction, the median ones passing through the stalk. Alcoholic ammonia was used for clearing in this series.* The second set (O) was cut from a fruit which was also compressed in a direction normal to the stalk. The fruit was cut transversely. These preparations were cleared with a warm mixture of alcohol and formalin. The third set (II) is only represented by a few successful preparations. The fruit was here compressed vertically and the remains of the stalk and stigma are seen on one side of some of the sections. The sections were treated with the sodium sulphite method, but the form and the relations of the stigma were studied before chemical treatment was commenced. Other fruits were cut with less successful results.



TEXT-FIG. 8.—*Caytonia Sewardi*. Longitudinal section of a fruit. Camera lucida drawing to show the outlines of the seeds from a section in series Z. The remains of the megaspore membranes are indicated in the centres of those seeds in which they are seen, and the areas occupied by the cutinised cells associated with the stigma are dotted. × 50. (*Cf.* Pl. 13, fig. 32.)

In each series the heavily cutinised outer wall of the epidermis and the cells of the stigma are clearly visible without chemical treatment. The cuticle of the epidermis seems to have been almost entirely confined to the surface walls and was from 7·5μ to 11μ thick. In the case of fruits compressed longitudinally, the epidermis shows a complex series of small folds due to the compression, but in the fruits compressed laterally the folding is mainly restricted to the apical portion.

The seeds did not fill up the entire space within the epidermis of the fruit. In sections cut longitudinally there is a considerable space at the distal or apical end of the fruit which is much compressed and appears in sections as a narrow tongue-like projection (*cf.* Pl. 13, fig. 32), sometimes rather enlarged at the end. This seems to indicate that the original fruit had a fairly thick fleshy wall surrounding the ovary. There is very little evidence as to the structure of this wall, but tangential sections through it have been prepared which seem to show the outlines of large rounded cells with irregular, somewhat thickened walls, which may have been formed from a fleshy tissue (Pl. 13, fig. 28.)

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* See page 303.

Unfortunately, little or no structure can be detected in the stalk. My method does not seem to differentiate tissues which were not strongly thickened, and we may consider that the vascular elements, which must have been present and of which an indication is seen in one slide, were not very heavily lignified.

The stigma can be readily distinguished in sections passing through it on account of its cutinisation. As in *Gristhorpia*, the surface of the small stigmatic flap was heavily cutinised and also the adjacent tissue between the stigmatic flap and the stalk. This is well seen in Pl. 12, figs. 18, 20, where the cutinised walls appear light in colour and translucent. The stigmatic opening is seen to be very much shorter than in *Gristhorpia*, but in median section the zone of cutinisation extends some distance into the fruit, the cells gradually becoming smaller and their walls thinner. Longitudinal sections through the stalk in laterally compressed fruits show this cutinised zone as a semicircular flange (Pl. 12, fig. 18) with ray-like internal extensions spreading upwards towards the region of the seeds. There are indications that the cutinisation may have extended as far as the micropyles of the lowest pair of seeds.

Internal Arrangement of the Seeds.

The central portion of the fruits is occupied by a compact mass of seeds closely pressed together. In sections of series II the seeds have been displaced from their original position, and one of them lies close to the inward extension of the stigmatic cells (Pl. 12, fig. 20). There was no central placenta and there is no trace of any division of the ovary into loculi. There seems little doubt that the seeds were attached in some way to the fruit wall (parietal placentation), but in no case can their attachment be now clearly seen. Probably most of the seeds were detached during the process of compression, but in the series Z they are still seen to be arranged in a very regular manner (*cf.* text-fig. 8). Here we see sections of seven seeds, those next to the stalk being arranged regularly in pairs and the odd seed filling in the space between the top pair. This must clearly bear some relation to the original disposition of the ovules. The lower seeds are cut obliquely, the upper ones almost transversely, and where traces of the micropyles can be seen they occur at the end next to the stigma. It seems likely, though I have been unable to ascertain this by direct observation, that the ovules were attached in two rows to the fruit wall on the dorsal side in the plane of the pedicel, as shown in the diagram (*cf.* text-fig. 7). The outlines of the seeds, as seen through the fruit wall, confirms this supposition. It is difficult to account for the arrangement of the seeds seen in the series Z by any other supposition, and it is unfortunate that the series is so incomplete as to render confirmation of this view impossible.

Structure of the Seeds.

Most of the successful preparations of fruit sections show something of the structure of the seeds, and it seems certain that their testa was composed of woody or stony cells which have suffered but little deformation (Pl. 13, fig. 29). Almost all the sections are cut through the seeds in oblique directions, but a few are almost transverse or almost longitudinal. The seeds no doubt owe their flattened shape largely to compression, there is some evidence that they were originally more rounded in section. On the other hand, some irregularities in the disposition of the fibrous layer and folds in the megaspore membrane lend support to the view that the original seed was originally somewhat flattened before being buried and further compressed.

The Testa.

Although the examination of the apical part of isolated seeds which have been macerated suggests that there may have been two integuments, we can only see in most sections a single structure composed of three distinct parts, recalling somewhat strongly the structure of the integument of the Palæozoic Pteridospermous seed *Conostoma*, and we may adopt the nomenclature used for that seed.*

(*a*) *The Blow-off Layer.*—This layer is only seen in places where the seeds abut on the fruit wall, and has entirely disappeared where two seeds touch one another (*b*. Pl. 13, figs. 25, 30). It was, therefore, probably of a soft nature, easily squashed by pressure between the hard parts of the testa, but being harder than the fleshy fruit wall, it preserved its shape fairly well in contact with the latter, and more especially at the ends of the seeds where not in the direct line of pressure. It is clearly visible in all of the preparations made by the alcohol and formalin method of clearing (series O). It is occasionally seen in series Z, where the clearing has not been allowed to proceed too far, and it is practically invisible in series II after the hydrochloric acid and sulphite treatment. This probably indicates that it was somewhat similar to the fleshy fruit wall in its chemical nature.

It appears to have consisted of a single layer of cells of more or less rectangular shape 30μ by 15μ as seen in surface view and about 11μ deep. In some cases there are indications that the outer wall was dome-shaped or slightly papillate, and in series Z the walls appear somewhat thick (Z1).

A very curious and noticeable point is that it was cutinised on its inner side, and this alteration spread a short way up the radial walls. Consequently in fully cleared specimens the palisade layer appears to have a well cutinised wall with short peg-like projections upon it (*t*. Pl. 12, fig. 19). No trace of this layer remains in the isolated seeds except these small projections on the outer cuticle, and we are justified in regarding it as a layer of cells of a transient character, somewhat similar to the blow-off layer of the seeds of *Conostoma* and of some Cycadeoideas.

(*b*) *The Palisade Layer.*—This was a layer of thick walled cells, and in all specimens it appears intact and apparently undistorted. In sections cut tangentially to the surface the cells appear as fairly regular hexagons about 25μ across, and the same appearance was noted when the isolated seeds were macerated and treated with

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* Oliver and Salisbury (1911).

ammonium carbonate solution. In transverse and longitudinal sections of the seeds these cells appear as a fairly regular series about 32μ deep. In transverse sections their middle lamellæ (*cf.* Pl. 12, fig. 20 ; Pl. 13, figs. 25, 30) are seen to radiate outwards and are inclined to the surface, an appearance no doubt accentuated by the compression of the seeds. Towards the ends of the seeds they appear to become narrower and more elongated, but this may be due to the obliquity of most of the sections. For the same reason we sometimes see two rows of these cells separated by a zig-zag line.

In the centre of each cell a small round dot is seen, which probably represents the lumen, the cell wall being the brown material lying round it and inside the middle lamella.

This layer seems to be absent at the base where the seed was attached to the placenta. Such a layer of regular thickened cells, which was probably woody or stony, can be closely compared with the hard testa of *Conostoma*, and also with the corresponding layer of cells in the seeds of the Bennettitales.

(*c*) *The Fibrous Layer.*—The layer of cells which gave rise to the peculiar fibre "spicules," which we noted round the megaspore membrane in macerated seeds, is the innermost part of the hard integument. It is clearly seen in preparations made by all methods of clearing (*f.* Pl. 13, figs. 29, 30). In fully-cleared sections of series Z, the cell walls have almost disappeared, but the central spicule-like structure is left, and is very clearly seen after staining with gossypamine (*f.* Pl. 13, fig. 31). Similar structures can be obtained by macerating the fibrous elements of some modern plants, and there can be little doubt that the cells from which they were produced were also strongly thickened fibres or stone cells.

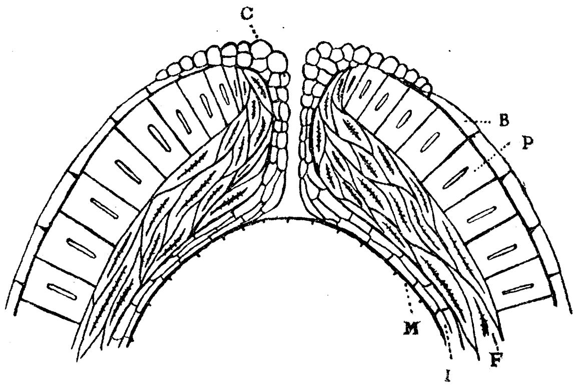
In series O the middle lamellæ are visible in this tissue and the cells are seen to be long and narrow with pointed ends. They were at least 70μ long and about 8·17μ wide, but they probably were shorter towards the ends of the seeds. In transverse sections they often have a hexagonal appearance. The lateral points on the "spicules" probably indicate the presence of a considerable number of simple pits when young. They often seem to abut immediately on the megaspore membrane, though it is probable that there was originally another more internal layer of cells which disappeared when the hard fibrous layer was tightly compressed against the highly cutinised megaspore membrane. If there was any vascular tissue in the seeds it probably took the form of a few tracheids embedded in this fibrous tissue. I have searched very carefully but have failed to find any traces of bundles in transverse sections. In a longitudinal section of a seed, I have observed what may possibly be the remains of two minute tracheids with scalariform or annular thickening, but I have no confidence that these are really the remains of tracheids and not parts of a "spicule" whose lateral projections often produce an appearance not unlike that of vascular tissue. These fibrous elements appear to form most of the integument at the base of the seed, and they extend upwards to form a narrow zone surrounding the micropyle, their thickening probably being less developed in this region.

Indications of an Inner Integument.

In some sections the fibrous layer appears as though separated from the cutinised megaspore membrane by a narrow space which seems to have been occupied by a few cells which are now crushed beyond recognition. In many preparations a split occurs in this region during the clearing processes, and occasionally the membrane of the megaspore when separated from the fibrous cells retains a film of brown material, perhaps representing the remains of crushed cells, attached to it. At the micropylar end of the seed the same membrane in several cases is seen to be distinctly separated from the fibrous cells, and often has small outwardly projecting points, as though the cells which had been compressed against it were cutinised.

There seems to be little doubt that near the upper end of the seed a thin layer of cells surrounded the megaspore and that it was continuous with the cells lining the tube of the micropyle. We have, however, nothing to indicate whether these cells should be regarded as a thin, perhaps fleshy, coat of the hard testa, which would then have not three but four layers of different structure, or as an alternative we may regard them as the remains of a second, thin, inner integument composed of soft tissue and comparable to the inner integument in *Gnetum africanum*.

We have seen that the macerated seeds of *Gristhorpia* present indications of the existence of two integuments, but no fibrous layer was there present. The macerated seeds of *Caytonia*, on the other hand, afford no such indication, apart from the canopy of cutinised cells round the micropyle. I consider that a second, thin, inner integument was present, though the point cannot be regarded as proven. It is admissible in dealing with these seeds to postulate the former existence of such a layer, even though it cannot be detected round the body of the seed, for we should expect delicate tissue to be always crushed out of recognition when enclosed between two hard or cutinised tissues.



TEXT-FIG. 9.—*Caytonia Sewardi.* Reconstruction of the apical part of a seed from information supplied by sections and macerated specimens. × 100. B. Blow-off layer. P. Palisade layer. F. Fibrous layer. C. Cutinised cells lining micropyle and forming flange at the exterior. I. Parenchymatous cells possibly representing inner integument. M. Megaspore membrane (*cf.* Pl. 12, fig. 19 ; Pl. 13, fig. 26).

The Megaspore Membrane.

The megaspore membrane is seen as a narrow band lying in the centre of the seeds, often in a somewhat irregularly crumpled manner (*e.* Pl. 13, figs. 29, 30). It was strongly cutinised and stains readily with gossypamine, and also with Sudan III. The remains of the cells, which are seen in surface-view in macerated specimens, can seldom be made out. We can usually see that the band has a double structure, a fine line of brown material lying between two cuticularised boundaries and representing all the original contents of the megaspore. When sections are very fully cleared the membranes from the two sides of the megaspore which have been crushed together, separate. Each has a thickness of about $1 \cdot 5\mu$.

The Micropyle.

Few sections have been found in which the remains of the apex of the megaspore can be seen together with the micropyle. The best example is shown in Pl. 12, fig. 19. The remains of four seeds are lying in close contact and the two centre ones are cut through almost apically. The right-hand one has been fractured and its structure is obscured by the presence of a line of celloidin in the fissure. The section of the left hand central seed is much more perfect and nearly median. Here the remains of the megaspore membrane is seen to be double below, but above it thickens out and its double nature is no longer seen; it passes up into a number of rounded cells, the lower ones being strongly cutinised.

These cells are no doubt the lining of the micropylar tube which we saw in macerated specimens. The section is not median, so that they appear to decrease in number towards the outside of the seed where the cutinised wall of the palisade layer with its projecting points is seen. The flange of the micropyle and the blow-off layer have disappeared. The curious five-pointed fragment of cutinised material seen near the apex of the seed is worthy of note, but its significance is unknown. Near the micropyle traces of the fibrous layer are seen, which evidently extended to the outside of the testa round the micropyle, but the spicular structures are less well developed, and probably the cells of the fibrous layer were less thickened at this point. We may also notice in this seed that lower down there is a space between the fibrous layer and the megaspore membrane in which there appear some indefinite traces of thin-walled cells which may be regarded as the inner integument.

Another section (Z.10) which is not cleared so much shows a cylindrical zone of thin cutinised cells about 45μ wide at the top of the megaspore membrane, with a thin extension tapering upwards to the tip of the micropyle. The cells composing it are very irregular in shape and size (probably partly due to the plane of the section), the central ones being larger and more elongated. This section passes very near to the apex of the micropyle, and the cells of the apical flange appear lightly cutinised all round, as we saw in the macerated specimens of isolated fruits.

The adjacent seed in this section is cut nearly apically, and again points to the original paired arrangement of the seeds inside the fruits. Other sections in the same slide show the cutinised cells at the top of the megaspore.

No good sections have been found in series O showing the micropyle, though in one place some of the cells at the apex of the megaspore membrane have been observed. It is probably unwise to expect to see many details of structure in a delicate plant which has undergone the compression and alteration to which these seeds have been subjected, so that we cannot hope to know whether there was any structure at the base of the micropyle corresponding to a gymnosperm pollen-chamber or to a lagenostome.

There is no clear evidence as to the exact structure of the tissues at the top of the micropyle. The macerated seeds show a flange-like zone of rounded cutinised cells continuous with and similar in shape to those lining the micropyle, and the sections show some remains of similar cells cutinised all round, and not only on the inner side, as in the case of the blow-off layer. But I cannot determine whether the apical flange was continuous with and formed from the blow-off layer or whether it was superposed upon the latter. The sections are all very imperfect at this point, and I have been unable to trace the blow-off layer near the micropyle. For the present, I rely on the great difference in shape of the cells forming the flange and those of the blow-off layer, and regard this flange as the extension of the hypothetical inner integument which was superposed upon the blow-off layer (*see* text-fig. 9).

Fertilisation.

The presence of winged pollen grains on the stigmatic surface of *Gristhorpia* indicates that pollination was effected by wind in that genus. In *Caytonia* the stigmatic surface is considerably smaller, but we have the same type of structure, and the stigmatic surfaces are somewhat papillate (Pl. 12, figs. 18, 20). The cells are strongly cutinised, and I interpret this as indicating that these cells when young contained sap which was rich in fats and sugar on which the pollen tube may have been nourished. The rays of cutinisation extending inwards, would probably mark the path of the pollen tube in its first stages of growth inwards. The question may now be asked, How did the pollen tube reach the micropyle? It has been suggested that chalazogamy is a primitive character in Angiosperms,* and such a process is possible here though the ovules possessed such highly specialised integuments. We, unfortunately, know nothing of the tissue which the fruit contained in addition to the ovules, but some indications have been observed which suggest that there may have been paths by which the pollen tubes were guided to the micropyles.

In the Z series of sections, where the stigma is cut through longitudinally, we see some of the ray-like extensions of the cutinised stigmatic cells cut through at a short distance from the stalk. Connected to these are some fine strands of cuticle extending up the sides of the fruit wall, and in several places appearing continuous with the remains of the seeds. In some slides they are like the crushed remains of a strand of elongated

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* *Cf.* WETTSTEIN (1911), p. 475.

cells, in others a single membrane with peg-like projections is seen. In no case, however, do these meet the testa (or the remains of the inner wall of the blow-off layer) near the micropyle, but generally towards the side of the seed. On the other hand small fragments of cutinised material may be found near the micropyle. It seems worth suggesting that these structures may (*a*) either mark the path of a chalazogamous pollen tube, or (*b*) that they may be the relics of fine tubular extensions of the micropyle and inner integument (*cf. Ephedra trifurca**), which, during the life of the carpel, grew out until they were in contact with the cells of the stigma, and down which the pollen tube passed, but which were ruptured during the growth or during the compression of the fruit. There is little evidence for the second view, and the examination of the macerated seeds gives it no support, but the pointed projecting piece of membrane in Pl. 12, fig. 19, near the micropyle, might conceivably be derived from a structure of this nature, though it also may be simply a part of the apical flange which has been rubbed off the testa. The presence of these fine cutinised strands inside the fruit and connected to the stigma seems, however, a fairly definite feature, and one which is worthy of note.

Comparison of Caytonia with Gristhorpia.

The foregoing description shows that there are many points of similarity between the two forms. They are evidently allied, and must be regarded as belonging to the same family, if not to the same genus.

In both cases we have megasporophylls constructed on the same pinnate plan, with the " carpels " formed from pinnæ, and the main axis showing in its cuticular structure traces of a dorsiventral construction. The carpels enclosed numerous ovules, probably with parietal placentation, and the carpel wall seems to have been formed by the overarching of the fertile lamina of the pinnæ. The stigma was formed from the tip of the lamina at the point where it touched the stalk, and it was covered by papillate cells which became strongly cutinised in the fruit. The seeds were small ellipsoidal or somewhat flattened structures, probably with two integuments, originally covered with an evanescent layer of elongated cells, below which was a harder layer of cells which were polygonal in surface view. Both had a well-cutinised megaspore membrane and a small micropyle lined with cutinised cells. The fruits of both types were probably somewhat fleshy when ripe.

The question then arises : Should the two forms be placed in the same or in different genera ? This is not an easy problem when we have to deal with plants which are quite new and unique in type. We have no knowledge of the range of structure which existed, or of the systematic value of the various characters. There are important differences, and the consideration of these has led me to adopt separate generic names.

Differences have been noted in the form and structure of the epidermal cells of the axis and of the fruit walls. Next there is a distinction between the form and size of

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* LAND (1904).

the stigmas in the two types. *Gristhorpia* has a much wider and larger stigma which is easily seen in hand specimens, while the stigma of *Caytonia* is almost invisible, save in sections or in very favourably preserved examples. The two forms seem to show different stages in the evolution of the stigma. It has been shown above that there are reasons for believing that *Gristhorpia* possessed a very large number of ovules, arranged on the carpel wall without regular order, while *Caytonia* had 6–8 ovules arranged in two rows. In seed structure *Caytonia* resembles the Pteridosperms and other Gymnosperms in having a strong, stony, compound testa, so that the seeds are visible through the wall of the compressed ripe fruit. *Gristhorpia*, on the other hand, seems to have lost this character. Its seeds were certainly devoid of any fibrous tissue, and were probably of a softer and less stony nature. The details of the structure of the micropyle and apex of the megaspore membrane were different in the two cases, and these may well have been accompanied by important differences in original internal structure. The apical rupture of the more fleshy *Gristhorpia* fruits often provides a ready means of diagnosis in the field.

It seems to me that the above differences are too great to be considered of merely specific importance, and that they justify the course which I have adopted in creating two new genera.

Male Flowers, *Antholithus Arberi* sp. nov.

The discovery of pollen grains of a very characteristic shape on the stigmatic surface of young fruits of *Gristhorpia* has perhaps enabled me to identify the male flowers of this genus. In 1922, I found at a place in the Gristhorpe plant bed, about 50 yards away from the spot at which most of the specimens of *Gristhorpia* and *Caytonia* were obtained, several specimens showing slender axes with short lateral branches on which elliptical, anther-like structures were borne. These were not associated with fruits, but in six of the seven hand specimens *Sagenopteris* leaves are found, the only other associated plants which can be identified being twigs and male cones of *Pagiophyllum Williamsonii* (Br.). The specimens were freed from the matrix a little, and in some of the small chips parts of their structure are seen very clearly (*cf.* Pl. 14, fig. 36). They were readily detachable from the matrix, and consequently provided good material for examination by maceration methods.

These structures are undoubtedly identical with the specimens in the Sedgwick Museum, Cambridge, one of which was originally figured by Phillips,[*] and which have subsequently been carefully re-figured and described by Prof. Seward,[†] as *Antholithus* sp. The latter author was unable to obtain any spores from them, but the preparations made from the new material show that they produced the characteristic winged microspores which were first found in *Gristhorpia* stigmas.

The new specimens are all fragments of more or less mature inflorescences (Pl. 14,

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[*] Phillips (1875), Pl. 7, fig. 23.

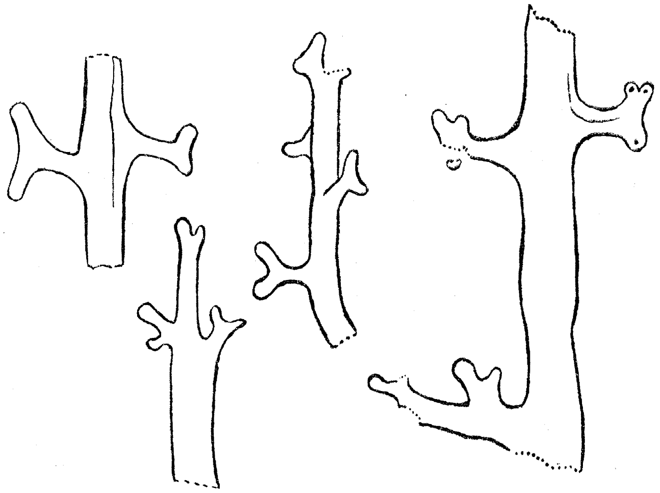
[†] Seward (1919), pp. 51–52, fig. 654.

fig. 35), in some of which the anthers have already dehisced. Neither apex nor base of the inflorescence is clearly seen. The most complete specimen (Pl. 14, fig. 33) shows a portion of an axis 15 mm. long, from which seven or eight lateral branches arise. It is impossible to determine how these were arranged in the original structure, but in the flattened condition they appear to be sub-opposite. The central axis was a slender structure $\frac{1}{2}$–$\frac{3}{4}$ mm. broad, and the lateral branches are still thinner. Both show a certain amount of longitudinal wrinkling, as in the case of *Gristhorpia* and *Caytonia* peduncles, probably due to the compression of a tissue which was originally of a soft and delicate nature. From other specimens, cuticular preparations were made to show the structure of the epidermal cells of the axis.

The best preparation (Pl. 14, fig. 34) shows that the epidermal cells of the two sides of the axis were slightly different, as in the case of the axis of *Gristhorpia.* On one side the cells are slightly wider and larger than on the other, again suggesting that the male inflorescence had a dorsiventral nature. The cells were arranged in regular longitudinal rows and were rectangular or fusiform in shape. In form and size they were almost identical with the cells in the stalk of a *Gristhorpia* infructescence, as seen in the preparation GY 6. No stomata can be made out, but occasionally some small, darker cells are seen which appear to have been of the nature of papillæ. Somewhat similar structures have been noted on some *Sagenopteris* leaves.

Preparations have been made from some of the small side branches or floral axes, but in these the cells are very lightly cutinised, and no additional information is given.

Five fragmentary specimens showing axes from which the stamens have been detached have been studied, and their outlines are shown in text-fig. 9A and Pl. 14, fig. 37. The lateral branches are characteristic short structures, which usually seem to fork at a distance of 1–2 mm. from their point of origin. Their arrangement does not seem

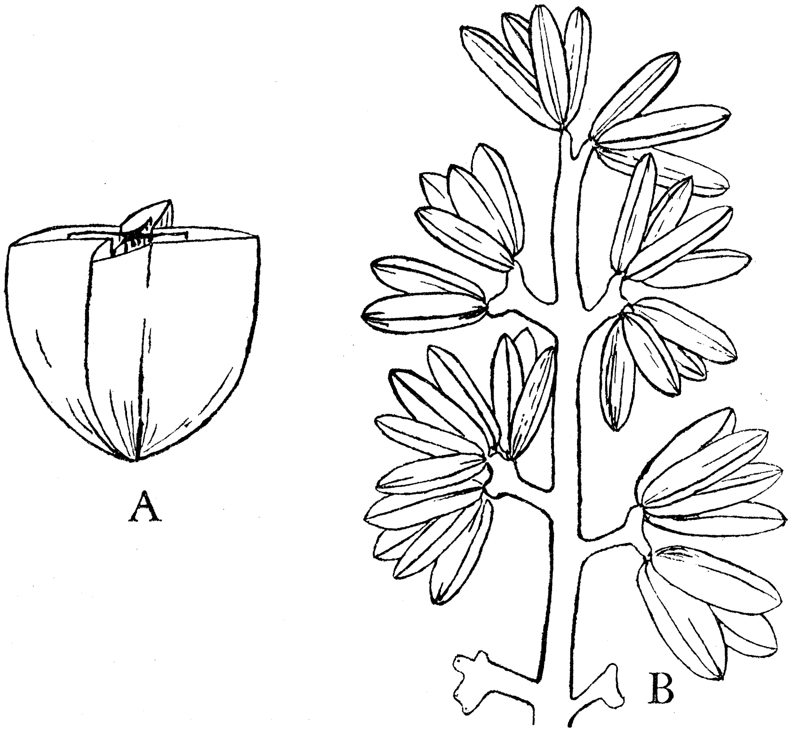


TEXT-FIG. 9A.—Drawings of parts of microsporophylls from which the stamens have become detached, showing the characteristic lateral branches. × 7.

referable to a spiral plan and they may better be described as sub-opposite, but, as will be seen from the figures, they do not show any regularity in either arrangement or form.

One of the best preserved specimens (GRA 2) shows these lateral branches, which appear to have forked more than once, and at the tips of some of these short ultimate segments small circular scars are seen. There is little doubt that these were the points at which the stamens were attached.

Unfortunately, no specimen shows clearly the number or exact arrangement of the stamens. These are all more or less embedded in the matrix and frequently lie on top of each other, so that no single specimen shows a complete group. It seems probable that the number of stamens in each was about 3–6. In the best-preserved examples there is no indication of the presence of bracts or perianth, though some minute projections have been noted on the axis, which might possibly be interpreted as the bases of small scale-like bracts.



TEXT-FIG. 10.—*Antholithus Arberi.* A. Part of a single anther showing the four lobes. Reconstructed from a macerated specimen. × 16. B. Reconstruction of part of a male inflorescence. × 4.

The stamens were from 4–7 mm. long, sessile or with a very short, delicate filament. The anthers are elliptical structures, 1·5–2 mm. broad, with a mucronate tip. They had a well-marked, four-winged form when living, and in the hand specimens one wing is often seen lying above the middle of the two others and more or less surrounded by matrix (Pl. 14, fig. 36, *a*). When specimens are removed from the matrix cleared with hydrofluoric acid and macerated, the four-winged structure becomes quite clear (*cf.* text-fig. 10, A).

There is no definite distinction observable between the connective and the pollen sacs, but it seems fairly certain that one pollen sac occupied each wing. Microscopic examination of the surface displays a somewhat striated appearance which, on examination with a high power, appears to be due to the thickening of the walls of the epidermal cells.

Macerated specimens (Pl. 14, fig. 39) show that the stamens had a delicate outside cuticle and that the epidermal layer was formed of narrow fusiform cells. In some preparations, indications are seen of a layer of larger and more strongly thickened fibrous cells below the epidermis. The epidermal cells in the grooves between the four wings are thinner and several of the specimens seem to indicate that longitudinal dehiscence took place in this region. From all the preparations made large numbers of almost mature pollen grains were obtained (Pl. 14, fig. 40), but it has not been possible to determine the manner in which these were produced from the pollen mother cells.

Pollen Grains.

The pollen grains have the very characteristic shape already referred to (*cf.* p. 308) of a central cell lying between two wings. The central cell appears to be more or less overlapped by the wings and has a clear, transparent wall. The wings show a very fine granular appearance, probably due to the presence of minute projections on the wall (*cf.* Pl. 14, fig. 38). Unlike the pollen grains of *Pinus*, the wings are symmetrically placed on either side of the central cell in all specimens seen. The longer axis of the grain (passing through the wings) is generally between 22μ and 28μ, the width of each wing being about 8μ. The shorter axis measured through the central cell is from 15μ to 19μ. The wings seem to have expanded during development, and in the case of the grains found on the stigma of *Gristhorpia* the total width of longer axis was about 30μ. In the smaller spores the wings appear like crescents on either side of the central cell, but later the concave side becomes straight and they tend to bulge a little above the central cell. There seems no reason to doubt that they were structures identical in nature and in function with the wings of the *Pinus* pollen grain.

It is interesting to notice here that very similar microspores have been described and figured by NATHORST* from the shale beds in the Hör sandstones of Southern Sweden, which are of Rhætic age. These showed clearly the lateral sacs or wings, arranged in the same manner as described above and with the same finely granular surface. NATHORST found that his examples of this form were separable into two groups, one of larger spores 100–108μ broad, and a second group which were similar in size to those now described and 29–36μ broad. Being ignorant of the plants from which these spores were derived, NATHORST considered the larger spores as evidence of the existence of the genus *Pinus* at the end of the Triassic period, while he regarded the smaller spores as derived from an unknown plant. The pollen grains now described are so characteristic

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* NATHORST (1908), p. 12, Pl. 2, figs. 53–58.

that it seems reasonable to conclude that NATHORST'S work indicates the existence of plants closely allied to the *Caytoniales* in Sweden at the close of the Triassic times.

While it cannot be conclusively proved that the male flowers described above were borne by the same species of plant whose fruits have been described as *Gristhorpia*, yet the probability that such was the case is considerable. A fair number of microspores were found on the *Gristhorpia* stigmas with only two other grains of foreign (?) pollen. Winged pollen grains have been recently found sticking to some *Sagenopteris* leaves, but they have never been found adhering to the exterior of the *Gristhorpia* or *Caytonia* fruits. It is very unlikely that pollen grains could find their way to the stigmas after the severance of the fruit from the parent plant and remain attached there. The evidence for connection derived from the occurrence of pollen on the stigma is well supported by some of the details of the cuticular structures of the axes which bore the stamens and carpels. The size and shapes of the epidermal cells from both the male axis and the younger female axis are almost identical. The curious feature that both of these axes tend to show some degree of dorsiventrality in the structure of their epidermal cells, is also a strong point for comparison. On the other hand, I have been unable to detect any feature which contradicts this view.

But while it seems probable that these microsporophylls belonged to the same type of plant whose carpels and fruits have been called *Gristhorpia*, we do not know that they were borne on Gristhorpia plants exclusively, and not on Caytonia bearing plants as well. In view of this it appears to be undesirable at the present time to designate them as the male inflorescences of *Gristhorpia Nathorsti*. As already mentioned, it seems to me desirable to retain the generic name *Antholithus* for these remains, giving them only a new specific name and calling them *Antholithus Arberi*.

We may then conclude that the flowers of the Caytoniales were unisexual and that the male and female flowers were borne on separate inflorescences. There is no evidence for the existence of a perianth in either case, or for the presence of any noticeable bracts. It seems likely that the megasporophylls and carpels were borne in a pendulous position on slender branches and that pollination was effected by the agency of wind.

THE LEAVES OF THE CAYTONIALES.

Since we find numerous examples of the fruits and also of the seeds of *Gristhorpia* and *Caytonia* in the middle Jurassic beds at Gristhorpe Point, we may naturally expect that the leaves of the plants which bore them should be present also. There are no distinctly Angiospermous leaves known, however, from this locality, and there are but few leaf types which cannot be referred to their classes with some degree of certainty.

It is very unlikely that the portions of the fruiting branches, the fruits and the seeds which have been described above, should fall into the mud of the lagoon in which they have been preserved without a single leaf accompanying them, but, on the contrary, we should expect them to be accompanied by a moderate if not a considerable number of leaves.

In collecting at the locality it was soon noticed that where the fruits were found a particular type of leaf was very abundant, viz.: the type *Sagenopteris Phillipsi* (Brongn.). This is a compound leaf with a stalk on which 3–6 leaflets are borne in a more or less palmate manner (Pl. 15, figs. 50, 51), the nervation of the leaflets is very characteristic, each having a peculiar reticulate series of secondary veins, generally with a distinct midrib near the base (*cf.* Pl. 15, fig. 53). On account of their similarity to the recent Marsilia, these leaves have been generally regarded as belonging to plants of the Hydropterideæ, but without any more conclusive evidence than similarity in form. Observations in the field would point to a possibility of this type being the leaf of *Caytonia* or *Gristhorpia.*

On a matter as important as this, it is very unwise to trust to impressions gained in the field as to the association of plant structures, and though such observations have their value, they cannot always be relied upon. Is it not possible to state the evidence of association in a more convincing form? It seemed that something more definite might result from the examination of all the hand-specimens* in my collection which are of sufficient size to contain leaf remains in addition to the fruits. Consequently I tabulated the forms shown in each specimen on the same face as that on which the fruits lie. The few examples which show fruits only have not been included as they are all of small size. The results are as follows:—

	Total number of hand specimens.	Numbers of specimens showing fruits, etc., associated with						
		Leaves among which Sagenopteris is absent.	Sagenopteris.	Taeniopteris.	Pagiophyllum.	Nilssonia.	Cladophlebis.	Czekanowskia.
Gristhorpia	85	9	76	7	20	24	19	1
Caytonia	60	9	51	23	22	13	12	1
Antholithus Arberi...	7	1	6	...	3	...	...	...
Caytoniales	152	19	133	30	45	37	31	2

12 specimens showed no associated leaves and are not included in the above figures.

We see from the above table that there is a well-marked difference between the frequency of association of parts of the Caytoniales with *Sagenopteris* and with other leaves. The association of the fruits and anthers with *Pagiophyllum* is clearly accidental and the figures for *Taeniopteris*, *Nilssonia* and *Cladophlebis* probably show the result of chance. The association of *Sagenopteris* is, however, of a different nature, for in only 19 of all the specimens is this leaf absent, and its presence in 133 out of 152 specimens cannot be regarded as accidental.

It would appear, then, that there is a definite correlation between the occurrence of the fruits of *Caytonia* and *Gristhorpia* and of the leaves of *Sagenopteris*, and that their

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* Each piece of shale containing fruits, seeds, etc., is termed a hand-specimen.

association is very pronounced. The numbers of the specimens examined are sufficiently large to avoid the danger of a chance association, and this correlation must have some significance. It does not prove the original connection of these structures conclusively, but it suggests the case so strongly that the discovery of any further evidence would render such a connection highly probable.

We are, however, faced with a difficulty. Our studies of the fruits indicate that the Jurassic Caytoniales could be separated into two very distinct genera, equally common in the locality. From the analogy of modern plants we should expect each genus to have possessed a distinct type of leaf, but we apparently have in *Sagenopteris Phillipsi* only a single leaf-type. This difficulty is capable of resolution, because within the limits of this form we have a great variety of shape and some variety of structure.

Prof. SEWARD describes the species *Sagenopteris Phillipsi* (Brongn.), including the varieties *major* and *cuneata*, as follows*:— "Frond very variable, petiolate; in some forms the petiole bears four linear, lanceolate leaflets having a distinct midrib and oblique, anastomosing lateral veins; in other forms are shorter and broader, somewhat obcuneate leaflets without a midrib and traversed by spreading anastomosing veins." Some authors had previously made two species, *Sagenopteris Phillipsi* and *Sagenopteris cuneata*, but SEWARD concluded with BUNBURY† that it was reasonable to suppose that both forms of leaf were borne by the same species. The examination of the specimens which I have collected leads me also to the conclusion that it is impossible to separate the forms of leaf from one another on the grounds of shape; almost every variety can be found in the shape of the leaflets. The midrib may be absent or may be present at the base of the leaflets, or for a variable distance along them. If the leaflet lies in the matrix with the lower side uppermost, the midrib will be clearly seen, but if the upper side only is exposed the midrib may appear much less conspicuous. In such circumstances, the fact that we have only recognised one form-species of leaf does not rule out the possibility of its original connection with two genera.

But some further considerations have come to light. In the preparation of cuticles of these leaves it is found that, while some specimens seem to have had a firm texture and can easily be flaked off the rock (*cf.* Pl. 15, fig. 53), other examples were much more delicate and break up at once into smaller fragments. By the use of Canada Balsam and a glass slide as a transfer support, as in WALTON's method, it is possible to remove these more delicate leaves from the matrix and obtain cuticle preparations from them. It was found that such preparations showed an epidermal structure of a character different from those of the stouter leaves. The epidermal cells, instead of showing a distinct outline and straight walls, were scarcely visible, and on careful examination are seen to have had sinuous outlines of a totally different character. It is possible that here we are dealing merely with the sun and shade leaves of the same plant, but from the analogy with modern sun and shade leaves, it is more probable that the difference

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* SEWARD (1900), p. 163.

† BUNBURY (1851), p. 184.

has a more profound significance, and that the two types of epidermal structure indicate an origin from plants of two distinct species or genera.

After making this observation I carefully examined all my specimens again, with the view to ascertaining if we can divide them into two groups on the basis of external appearance, shape or venation; but it seems impossible to do so. In some specimens with very delicate cuticles the veins do seem to project more clearly from the fields of mesophyll between them, and the veins appear rather thinner, but these characters all seem to grade imperceptibly into the characters of the stouter leaflets. In some forms the petiole is more or less winged, but this also does not appear to be a specific character.

Rather more success was obtained by a comparison of the epidermal structure of the petiole in the various specimens available.

Structure of the cuticle and epidermis in Sagenopteris Phillipsi (Brongn.).

The structure of the cuticle was investigated in the hopes of proving or disproving the suggested connection of *Sagenopteris* with the Caytoniales fruits. It was thought that some similarity in the structure of the epidermal cells of the fruit wall and the epidermal cells of the leaf might be found; but, as already pointed out, the epidermis of the fruit appears to have possessed a very considerable amount of thickening, stomata were absent, and there were no papillæ, so that we can only use size, shape, and mode of thickening of the cells. It had also been found that the epidermal cells of the main stalks of *Gristhorpia* and *Caytonia* were not uniform all round, but those on one side were smaller, more strongly thickened and somewhat different in shape from those of the other side, suggesting origin from a dorsiventral structure. It seemed, then, that some light might be gained by comparing them with the structure of the epidermal cells in the petiole of the leaf.

The structure of the cuticles of *Sagenopteris undulata* Nath. and *Sagenopteris Nilssoniana* Br. has been described by HALLE,* and the Yorkshire leaves show the same general characters. I have made a number of preparations, and, except in the case of thin and delicate leaves referred to above, they show fairly uniform characters. The upper surface is markedly different from the lower; its walls are more strongly cutinised and stomata are absent; cells which lie above the veins are sometimes more elongated than the remaining cells of the cuticle, but frequently very little difference is seen. On the lower side the epidermal cells are sharply differentiated into a series of elongated, parallel cells below the anastomosing veins, and into isodiametric, irregularly arranged cells between the veins. The stomata lie in the latter areas alone and are comparatively few in number.

On close examination of the upper epidermis it is frequently difficult to make out clearly the outlines of the original cells, but in some preparations from smaller and presumably younger leaves the remains of the radial walls of the epidermis are seen. The cells are irregularly polygonal, with an average diameter of 0·02 mm. It would appear

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* HALLE (1910), pp. 5, 7, Pl. 3, figs. 1-10.

as though these cells became very considerably cutinised with advancing age. The thickening first appears on the upper surface and at the corners of the cells, so that the outlines of the epidermal cells appear less distinct and their lumina seem somewhat rounded. The appearance of other thicker cuticles suggests that the process of thickening did not proceed uniformly; some of the original radial walls became thick while others remain thin. Probably the cutinisation extended to the hypodermal cells, and in some places we have the appearance of two superposed layers of partially thickened cells. This thickening is especially seen in the elongated cells over the midrib, whose outlines soon lose their distinctness.

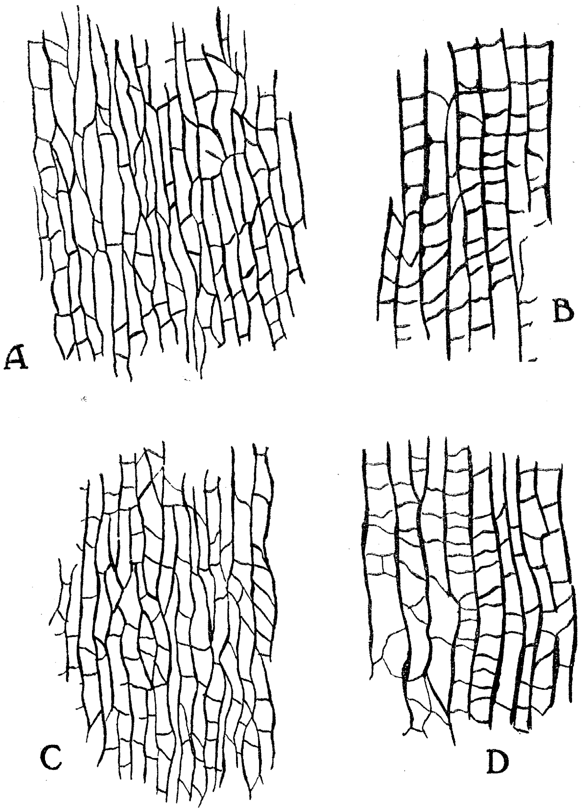
The character of the cells in this upper epidermis is very similar to that of the cells of the cuticle from the youngest fruit walls of *Gristhorpia* in the distribution of the thickening, in shape and in size, but the cuticles of the mature fruits are more strongly thickened. The cells of the fruit wall near the stalk are generally arranged in rows, with the longitudinal walls more strongly thickened than the radial walls, and this character is also seen in the epidermis above the midrib, especially at the base of the leaflets.

The lower epidermis of the lamina of *Sagenopteris Phillipsi* is composed of thin walled cells, slightly larger in size than the cells of the upper epidermis; above the veins they are often elongated or fusiform and are arranged in parallel rows. In the areas between the veins they are irregularly polygonal, without definite arrangement. Occasionally darker rounded cells are seen, which may have been short papillæ. The stomata number 15 to 20 per sq. mm., but they are not easy to see, and it is possible that this count is not very accurate. They are elliptical structures 0·045 to 0·057 mm. long when measured in a direction parallel to the slit. The guard-cells are not thickened as much as the surrounding epidermal cells, but stain deeper with Sudan III. They have no distinguishing markings and there are no special subsidiary cells.

The Petiole.

In my specimens the petiole varies in width between 1·5 and 3·5 mm. The broader specimens often appear to have a central conducting and mechanical portion, with a thin wing at either side. In the structure of the cuticle the petiole proves to be dorsiventral, the thickening being greater on one side than on the other and the cells different in shape. The amount of thickening and the cell shapes differ somewhat in different parts of the petiole and at different distances from the centre, but all cells are variations of the same general type. In most of the specimens examined the cells of the thicker (upper) side are arranged in regular longitudinal series, the longitudinal walls being more strongly thickened than the cross walls, which are somewhat irregular in their spacing, thickening and disposition. The cells of the thinner (under) side are much thinner, less regular, and vary in shape from rectangular to fusiform (*cf.* text-fig. 11, C, D). No stomata are present in the central parts of the petiole, where in both upper and lower cuticles there is a greater amount of thickening. A few stomata have been detected near the edges in some of the specimens which appear to be winged, and here also the cells are more isodiametric.

The cuticle structure of these petioles is very similar to that of the pedicels or main axes of the fruits of *Gristhorpia*, not only in their dorsiventrality, but in shape and method of thickening of the cells, as shown in text-fig. 11.



TEXT-FIG. 11.—Camera lucida drawings of cuticle preparations showing similarities in the epidermal structure of the petiole and fruit stalk. A. *Gristhorpia*, lower side. B. *Gristhorpia*, upper side (from G. 6). C. *Sagenopteris* petiole, lower side. D. *Sagenopteris* petiole, upper side (from S. 11). × 200.

An interesting specimen like that figured by SEWARD* in his catalogue as *S. Phillipsi* var. *cuneata*, in which the lamina takes the form of a single rounded leaf, instead of the usual three or four leaflets (Pl. 15, fig. 52), showed a somewhat different type of cuticular structure in the petiole. The cells were much more rectangular, on the upper side the transverse walls were closer and more thickened, and on the lower side the cells were broader, more regularly arranged and less fusiform. The structure of this cuticle is less like that of the axis of the fruits of *Gristhorpia* and more closely resembles the axis of *Caytonia*. The petiole of the trifoliate leaf shown in Pl. 15, fig. 51, was somewhat similar. (See text-fig. 12.)

When preparations were made from the lamina of these leaves it was found that the cuticles were very delicate and could only be separated with great difficulty. As in the other leaves with very delicate cuticles, it is not easy to make out any details of

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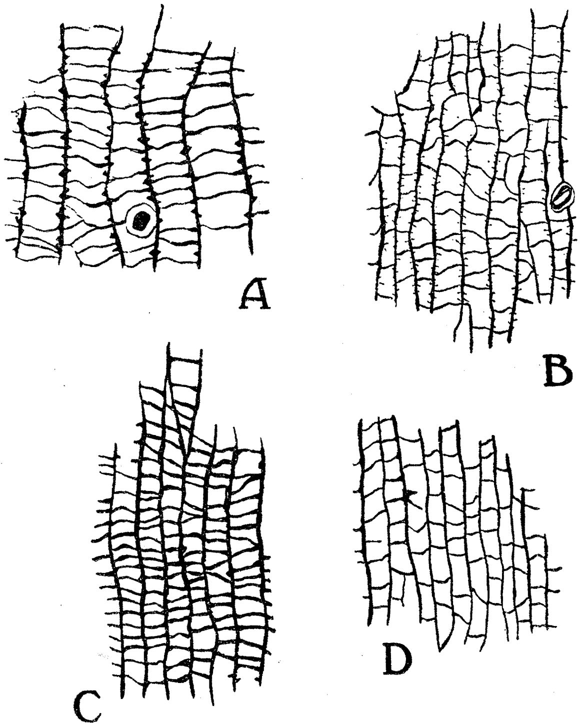
* SEWARD (1900), Pl. 18, fig. 3.

structure, but it could be here seen that the walls of the epidermal cells were not sinuous but straight.

No specimens have, of course, been found showing the organic connection of fruits with *Sagenopteris* leaves. I have, however, found an interesting specimen (CA 10) which provides further evidence for original connection and is worthy of description. The hand specimen shows part of an axis bearing *Caytonia* fruits (only the bases of some fruit stalks and the mould of one fruit are now seen); lying by the side of this is another stalk-like structure nearly 2 cms. long, of similar size and external appearance. Near one end we see some irregular scars, probably where leaflets were borne, and on one side a small deltoid pinna-like structure like a small leaflet of *S. Phillipsi* var. *cuneata* in organic connection with the main stalk or axis. The venation of the lamina is not very clearly seen, but a certain number of projecting veins can be seen and these fork and anastomose with one another as in the normal *Sagenopteris* lamina. The single leaflet seems to clearly establish the identity of the whole structure with the *Sagenopteris* type.



TEXT-FIG. 12.—Camera lucida drawings of cuticle preparations for comparison of the structure of the epidermis of the main axis of *Caytonia* fruits with that of the petiole of a *Sagenopteris* leaf of the short type shown in Pl. 15, fig. 51. A. *Caytonia* stalk, upper side. B. *Caytonia*, lower side; note rounded base of hair (from CA 24). C. *Sagenopteris* petiole, upper side. D. *Sagenopteris* petiole, lower side (from S 12). × 200.

A cuticle preparation was made from the lower end of the stalk (Pl. 15, fig. 49) and a preparation was obtained from the adjacent *Caytonia* axis. The two preparations showed a very close similarity. In both cases the epidermal cells were rectangular or sometimes triangular, the lateral walls have very characteristic thickenings in the form of small projecting points, and in both cases small rounded dark projecting papillæ are seen in the centres of some of the cells. The epidermal cells from one side are somewhat larger than those of the other. The only noticeable difference is that all the cells from the leaf stalk are somewhat larger than those of the fruit stalk, and both external and cuticular features point to their belonging to the same plant.

We have then some grounds for believing that possibly the leaves of *Sagenopteris Phillipsi* var. *cuneata* were borne on plants of the genus Caytonia, while the leaves of the ordinary form of *S. Phillipsi* belonged to the genus Gristhorpia.

Thus the results of the examination of the cuticle structure of the *Sagenopteris* leaves provide further grounds for connecting them with the *Caytoniales*. We see that the epidermal structure of their petioles matches closely that of the fruit stalks, both in its dorsiventrality and in cell form and thickening. The structure of the fruit wall in *Gristhorpia* is like that of the upper epidermis in the *Sagenopteris* lamina, though no lamina has been found with a structure that can be closely compared with the epidermis of *Caytonia* fruits. These points of resemblance may be coincidences, but when taken with the facts of association they justify us in saying that not only is the connection of *Sagenopteris* with the Caytoniales possible but *probable.*

Various arguments may be urged against this view and these may now be considered.

(*a*) On the grounds of the leaf shape and venation *Sagenopteris* is generally regarded as allied to *Marsilia* and the Hydropterideæ. Beyond these external features no further comparison is possible. The structure of the epidermis in *Marsilia quadrifoliata* is completely different. In specimens I have examined the recent leaflet shows almost the same epidermal structure on both sides, both having stomata.* The stomata occur above the veins and are not confined to the areas between them.

(*b*) *Sagenopteris* leaves have been found associated with structures which have an external similarity to the sporocarps of *Marsilia* at Bjuf and Hyllinge in South Sweden† in beds of Rhætic age, and also in beds of Middle Cretaceous age from the Blairmore Formation in Western Canada.‡ As will be shown later, there is no proof that the associated structures were really sporocarps, and not fruits of similar type to those here described. There is also no evidence of connection beyond that of the association of a few specimens.

(*c*) All known Angiosperms have leaves with a characteristic type of venation which does not agree with that of *Sagenopteris*. Leaves of a palmate form like *Sagenopteris* are commonly found among the recent Dicotyledons, but in this class the venation of the lamina of the leaflets is much more complex. We generally get a primary network of veins, and from these small branching veinlets project into the lamina filling the meshes of the network formed by the larger veins. In *Sagenopteris* all the veins are of uniform

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* *Cf.* NATHORST (1878), p. 18.

† HALLE (1910).

‡ BERRY (1922), p. 329.

character save the mid-vein or midrib. All the secondary veins anastomose with one another and none of them end blindly in the mesophyll, except at the margin. It may be noted, however, that the arrangement of the larger veins in many recent Dicotyledons follows a similar type (*e.g.*, species of *Ficus* and *Protea*, where also we have a series of meshes which become progressively smaller as the margin is approached.

During the ontogeny of some dicotyledon and fern leaves we seem to get a stage in which the main network of secondary nerves first appears, and this is followed by the formation of the smaller veinlets which end blindly in the lamina. In the evolution of the ferns* it would seem that a general sequence has been followed, leading from the open type to the forms in which there is a network with large meshes, and these become progressively filled by smaller and smaller veins. It is not unreasonable therefore to regard *Sagenopteris* as showing an early type of dicotyledonous structure, destined to evolve at a later date into forms in which the finer veins were developed within the meshes of the coarser network. If one examines the figures showing the nervation of some of the Lower Cretaceous (Potomac) Dicotyledon leaves such as are given by FONTAINE,† we see that the leaves of many forms have a nervation which could be derived from the *Sagenopteris* type by the enlargement of the lamina and the development of a series of smaller veins filling in the original network. Some of the earliest forms, *Rogersia, Proteæphyllum* and *Ficophyllum,* described by FONTAINE as occurring with a flora of Jurassic type at Fredericksburg, were especially of this type, and in describing *Ficophyllum* the author‡ commented on its archaic type of venation, and stated that he found it difficult to give any good characters separating these leaves from ferns.

At the same time it must not be forgotten that in the Stonesfield Slate remains of an almost contemporary leaf was found§ which, though not very well preserved, resemble more closely the recent Dicotyledons. Thus the evolution of the characteristic leaf form had probably already reached a higher stage than that indicated for *Sagenopteris.* In spite of careful and prolonged search no leaves of this type have yet been found in Yorkshire.

(*d*) A final argument against my view is that the mega- and micro-sporophylls of the Caytoniales appear to have been pinnately divided, while the leaves of *Sagenopteris* appear to be palmate. We can only say in reference to this that the *Sagenopteris* leaflets do not always spring from the same point at the apex of the petiole, so the four leaflets of the typical leaf may be regarded as representing two pairs of pinnæ very close together. *Sagenopteris* may have originally evolved from a form which had a regular pinnate foliage leaf, but in the course of development the number of pinnæ became reduced, as in some modern representatives of the Rosaceæ and Leguminoseæ.

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* BOWER (1923), p. 93.

† FONTAINE (1889), Pls. 140, 141, 144, figs. 2, 3.

‡ FONTAINE (1889), p. 291.

§ SEWARD (1904), Pl. 11, figs. 5, 6.

The existence of forms of *Sagenopteris* with three, two or one leaflet seems to indicate that this theory of reduction has a substantial foundation.

It may here be noticed that the petiole of *Sagenopteris* in some cases was winged, possessed stomata and probably mesophyll tissue in the wings. HALLE* figures examples of *S. undulata* where the petiole is still broader, more markedly winged than in my specimens, and where the leaflets are reduced to small dimensions. These small leaves may have been young specimens or of the nature of bud scales (*cf. Aesculus*), but they suggest a type of structure from which the Monocotyledon leaf may have originated on the lines indicated by the phyllode theory.

In concluding this section we may take the view that, while it cannot be regarded as definitely proved, there is a strong probability that the leaves of the Caytoniales were of the type known as *Sagenopteris*, and that it is more probable that *Sagenopteris* belonged to the Caytoniales than that it was the leaf of one of the Hydropterideæ.

COMPARISON OF THE CAYTONIALES WITH OTHER FOSSIL FORMS.

A few fossils of similar external appearance have been described, but so little is known of their details or structure that comparisons must be of a very superficial character. Several of them may be regarded as possibly related to the Caytoniales.

ZIGNO† figured and briefly described certain small spherical bodies found in association with his *Sagenopteris angustifolia* leaves. They are shown as having a diameter of about 4 mm., and were shortly stalked and covered with small points. No further information is available, but ZIGNO thought that the structures might possibly be sporocarps comparable with those of *Marsilia*. It seems equally likely that they were fruits of another form belonging to the Caytoniales.

NATHORST‡ in 1878 described and figured some small bodies bearing rounded humps which he found occurring with *S. rhoifolia* Presl. (*S. Nilssoniana* Br.) as possibly sporocarps. He investigated the cuticle structure of these bodies in detail at a later date, and arrived at the conclusion that they were probably the seeds of *Nilssonia*.§ The small humps were thought to be lumps of resin inside the seeds. These structures are somewhat similar in dimensions and shape to some of my fruits, and in my collection there are specimens which show a series of circular lumps very like those figured by NATHORST (Taf. 6, fig. 8). The structure of the cuticle of the seeds regarded as belonging to *Nilssonia brevis* (*cf.* Taf. 7, fig. 9) is not unlike that of *Caytonia*, while the preparations showing inner membranes, regarded by NATHORST as the remains of the nucellus, are very comparable to some preparations of what I regard as the megaspore membranes.

It appears to me that, while we cannot claim these seed-like structures as examples

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* HALLE (1910), Pl. 1, figs. 4-6.

† ZIGNO (1856), p. 186, Pl. 20, figs. 2, 3.

‡ NATHORST (1878), p. 18, Taf. 4, figs. 5A, 5B.

§ NATHORST (1909), p. 23, Taf. 7, figs. 6-13, 16, 17, 20; Taf. 6, figs. 1, 2, 8, 14-16.

belonging to the Caytoniales, yet it might be useful to reinvestigate them in the light of the present communication.

The next specimens to be mentioned are those described by HALLE* as *Hydropterangium marsilioides*. They were found at Bjuf and Hyllinge, in South Sweden, in association with *Sagenopteris*, and were regarded by NATHORST, HALLE and many others as sporocarps comparable with those of *Marsilia* and *Regnellidium*, and as evidence for the Hydropteridean affinities of *Sagenopteris*.

They are described† as " capsules, dorsiventral, flattened from the sides, oblong or bean-shaped, borne by pedicels, attached to one end of the capsule. Each lateral half traversed by ridges, parallel or diverging from the median portion of the distal edge." There is little evidence of their connection with *Sagenopteris* apart from association, and in this respect no statistical information is given.

The first point which arises in considering these structures concerns their identification as sporocarps. External similarity is certainly strong, but on maceration HALLE failed to extract either micro- or megaspore-membranes. Experience shows that when spores are present, even in a fairly young condition, they can generally be extracted by maceration, and the fact that Prof. HALLE did not find traces of any is a serious difficulty to our regarding these structures as sporocarps. He did, however, find traces of an " inner membrane," as well as obtaining the cuticle of the outer wall, and states that " it is not certain that this layer represents a real epidermis, as the cuticle—though of a considerable thickness—is too disintegrated to give a clear idea of its structure." No figures of this inner cuticle layer are given, and here, again, it is possible that it represents fragments of one or more megaspore membranes. When I first commenced the examination of *Gristhorpia* by maceration, I considered that the pieces of megaspore membrane which I obtained represented such an inner membrane as HALLE describes. It was only after the careful examination of a number of specimens that the entire megaspore membranes were obtained more or less intact, consequently it would be valuable for these fruits to be re-examined.

Until we have further information about their interior membrane we cannot be certain as to the nature and affinities of *Hydropterangium*. We certainly cannot regard it as a sporocarp without further evidence, as the danger of relying on similarities of external appearance is well known. Is any comparison with *Gristhorpia* possible ? From HALLE's Pl. 2, fig. 7, we see that the bean-like capsule was borne on a slender branching axis, that it was asymmetric, having a flattened edge on one side where an opening or hilum-like scar is shown, while the other side is rounded. The pedicel joins the capsule at one end, while the ridges and furrows radiate from the dorsal edge and not from the end, suggesting that the bundle entering from the pedicel followed for some distance the margin of the capsule before splitting up into transverse secondary branches.

This structure is somewhat akin to *Gristhorpia*, where we have a basal stalk and

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* HALLE (1910), p. 11.

† *Loc. cit.*

indications from the arrangement of the seeds that the vascular strand of the stalk probably continued up the dorsal side, though no trace of this strand has yet been observed, nor does the fruit wall show any lateral veins. HALLE'S *Hydropterangium* gave internal casts with a series of ridges and grooves running transversely across the structure. It is conceivable that these might have been produced by the replacement of a series of closely-packed flattened seeds by the fine-grained mud of the matrix. The ridges on these casts might then not represent the original placentæ, but the spaces between adjacent seeds which would first become filled with the matrix.

It has been shown that, while in *Caytonia* the stigma was closely approximated to the pedicel, it was more separated from the stalk in *Gristhorpia*. If *Gristhorpia* has the more primitive type of structure, there may have been a tendency for the stigmatic opening to shift from a lateral ventral to a basal position, and we might hope to find other examples in which the stigma occupied a still more lateral situation. I suggest the possibility that the flat ventral scar shown on the right of the capsule in HALLE'S Pl. 2, fig. 6, may be nothing less than a stigma, or an opening which was the precursor of the *Gristhorpia* stigma, formed in what may be its more primitive position.

There are, then, some grounds for believing that *Hydropterangium* may turn out to be another member of the Caytoniales. I believe that this can be easily proved or disproved when further material of the Swedish plant suitable for maceration has been obtained.

BERRY'S* sporocarps of *S. canadensis* are closely similar to HALLE'S form as far as can be ascertained from the description and figures, though the stalk and ventral face are not shown. They therefore occupy the same position relative to the Caytoniales, and we need not accept them as true sporocarps until they have been further examined.

The next specimen to be considered is the example in the MILLER collection in the Royal Scottish Museum, which was described by SEWARD and BANCROFT as *Strobilites Milleri.*† It also is associated with *S. Phillipsi.* In form and dimensions it closely resembles some of the more complete infructescences of *Gristhorpia* and *Caytonia.* The fruits—or seeds—have similar longitudinal wrinklings, but if the structures which SEWARD and BANCROFT believed to be seeds were actually fruits, no traces of seeds can be made out within them. Some of the lower " seeds " shown in the figure resemble *Gristhorpia* fruits closely, though when I examined the specimen I could not satisfy myself that any stigmas were shown. The specimen is not well preserved, but I think that it is probably a specimen of *Gristhorpia.*

Another species, founded on a single specimen, may also be mentioned as possibly related to the Jurassic Caytoniales. This is an example from the Lunz beds of Upper Triassic age found at Pramelreuth, in Austria, and described and figured by the late Dr. FRIDOLIN KRASSER‡ as *Pramelreuthia Haberfelneri.* The specimen showed an axis 40 mm. long and 1–2 mm. broad, bearing 15 stalked spoon-shaped structures,

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* BERRY (1922), p. 329.

† SEWARD and BANCROFT (1913), p. 882, Pl. 1, fig. 13.

‡ KRASSER (1917), p. 45, Taf. 1, figs. 5, 6.

thought by KRASSER to be microsporophylls. No preparations were made by maceration, but small lumps or granulations were noted on the sporophylls towards the top of the axis, while lower down they appeared striated. It was suggested that these surface markings were due to the presence of pollen sacs in different stages of development. I examined this species when I was with Dr. KRASSER in Vienna, and it appeared to be quite comparable with a *Caytonia* infructescence, though little could be made out for certain.

Another somewhat similar type has also been described by KRASSER as *Discostrobus*.* This genus was founded upon specimens from Transbaikalia. It consisted of an axis bearing stalked discs 3–5 mm. in diameter. These sometimes seemed to have a polygonal outline and appear to be more or less striated. Originally KRASSER was uncertain whether they were to be regarded as seeds or as microsporophylls, and the specimen figured as *Discostrobus corgunensis* appears comparable with some of my specimens of infructescences. Later† he described another specimen from the Lunz beds which seemed to show pollen sacs, but it is difficult to make out the exact structure from his description and figures, and also to reconcile them with the figures of the type specimen of his genus from Siberia.

Most of the forms mentioned above are so little understood, being based for the most part on the external features of one or two specimens, that their comparison with *Gristhorpia* and *Caytonia* can have little value. It is, however, useful to note that there is, at least, a possibility of fruit structures of the type seen in the Caytoniales being far more widely distributed than has hitherto been recognised. Palæobotanists naturally tend to try to relate rare or poorly preserved specimens to known plants, and in so doing may overlook some points of importance. It seems to me probable that, now the general features of this group have been described, we shall find that specimens referable to it occur in contemporary rocks in other parts of the world.

The male flowers of *Gristhorpia* may be compared to some extent with the interesting structures named by NATHORST *Antholithus Zeilleri*, and afterwards described in greater detail by ANTEVS.‡ Here we see microsporophylls or lobes of a fertile frond 5–7 mm. long divided up into three to five segments. The segments bore on the middle line of the lower side ovate pollen sacs, which were directed obliquely outwards and opened with a longitudinal fissure. The cuticles of the sporophylls were rather thick and possessed stomata. The pollen grains were ovate. While at first sight the Swedish species has some points of resemblance to our male flowers, in the forking microsporophyll and the large pollen sacs with longitudinal fissure, ANTEVS' detailed investigation seems to show that they were actually very different.

The pollen sacs of *A. Zeilleri* appear to have been simple unilocular structures not comparable with my four-lobed anthers, but we may note that microsporangia of a

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* KRASSER (1905), p. 39, Taf. 4, figs. 11-14.

† KRASSER (1917), p. 47, Taf. 1, fig. 4 ; Taf. 2, fig. 5.

‡ ANTEVS (1914), p. 10, Pl. 3, figs. 1-16.

more complex type have been described as occurring in the form described by KRASSER as *Lunzia austriaca.*[*] These were borne in large numbers on a large pinnate microsporophyll greatly differing in general appearance from the Yorkshire form, and regarded by KRASSER as the microsporophyll of one of the Cycadophyta. In spite of the differences in arrangement, it may be noted that the Lunzia pollen sacs were elliptical structures of similar size to those described here, and had somewhat similar longitudinal folds on their walls. They sometimes present the appearance of having four pollen sacs, and their outer walls were composed of similar but shorter elongated cells. Obviously, *Lunzia* was a plant of very different type, but is very worthy of mention as possibly showing parallel evolution of the pollen sacs.

In the collection of plants from the Lunz beds in the State Natural History Museum in Vienna I found a fossil labelled *Arthrophilia*, but which has not, I believe, been yet described, though collected in 1889. It seems to be more similar to my male flowers than any other examples I have seen, or which have been figured. The specimen shows the remains of a central slender stalk with tufts of what appear to be anthers or microsporangia on either side; their connection with the stalk is not clearly seen. Each group consists of four or five pollen sacs which in some places appear to radiate out from a central stalk and in other places are probably lying in a lateral position. Each pollen sac is about 3 mm. long. The preservation is not very good, and, unfortunately, I was unable to study the specimen in much detail or to make preparations. It is quite possible that it represents a structure similar to *Antholithus Zeilleri*, but in general form has points of similarity to the male flowers described here. Again, I regard this fossil as an indication of the *possibility* that plants related to the Caytoniales existed in one of the earliest of the Mesozoic floras which we know with any degree of completeness.

COMPARISON OF THE CAYTONIALES WITH OTHER SEED PLANTS.

(*a*) *Pteridosperms.*—Both male and female reproductive structures present a considerable number of features in which they may be compared with some of the Pteridosperms known to us.

In the first place we have seen that the arrangement of the carpels in opposite pairs on an axis suggests the foliar nature of the whole structure, and this suggestion is supported by the discovery that the cuticles on the two sides of the stalk were different, as is usually the case with leaves of Pteridosperms and Cycadean fronds. We have then a strong point of comparison with the Pteridosperms, where these seeds were borne on stalks on pinnate or bipinnate fronds.

The carpel wall enclosing the ovules and later becoming the fruit wall has no close parallel in Pteridosperm structures, but it may be compared with the cupule of *Gnetopsis,*[†] which probably enclosed from two to four seeds. There are no indications

[*] KRASSER (1917), p. 14.

[†] RENAULT (1885), 'Cours de Bot. foss.,' vol. IV., p. 180. OLIVER and SALISBURY (1911), p. 31.

that this cupule was closed in the Palæozoic form, and we may be almost certain that it was not.

In the structure of the seeds comparisons are possible, especially with *Gnetopsis* and *Conostoma*.[*] I believe that my seeds were somewhat similar in shape to those of *Gnetopsis* and slightly flattened, while they approach *Conostoma* in their integument structure. Their apical or micropylar part is, however, much simpler. We have no means of ascertaining if the Caytoniales possessed structures comparable to the *Conostoma* lagenostome, but from the macerated seeds it seems not impossible that some such structure was present. The special epidermal layer of Palæozoic seeds termed by OLIVER and SALISBURY[†] the blow-off layer, has its counterpart in the external layer of my seeds, for which I have adopted the same name. The projecting pegs left on the outer coat of the seeds in some cleared sections agree remarkably with OLIVER and SALISBURY's description and figures.

As in *Lagenostoma Lomaxi* and *Conostoma*, the testa of old seeds of *Caytonia* consists of two distinct kinds of elements, viz., an outer palisade layer and several layers of fibrous elements, which tend to increase in amount towards the micropyle. The remains of tissue round the micropyle in *Caytonia* is comparable with the soft integument of *Conostoma*, while the elongated cells lining the micropyle in that genus is suggestive of what we see in *Gristhorpia*.

One important point of difference may be noted, namely, that no traces of a vascular system can be made out in the *Caytonia* seeds, but this may be due to the method of preservation.

So far as our knowledge of the structure of *Caytonia* seeds goes, there appears to be much similarity with the structure of *Conostoma*. The long-plumed micropylar tube of *Gnetopsis* seems to be a very different feature, but we must remember that it is not certain that there were no micropylar appendages connected to the stigma in *Caytonia*.

The male "flowers" (*A. Arberi*) attributed to *Gristhorpia* may be usefully compared with the microsporophylls known as *Crossotheca*. Both were constructed in a pinnate manner with a narrow main stalk probably of foliar nature, but in the arrangement of the anthers and pollen sacs there seems to be much difference. The form of the pollen sacs was somewhat similar, but we know little of the structure of the microsporangia in either case. It seems probable that whereas *Crossotheca* synangia had two loculi, those of *Caytonia* probably had four.

So far as the available facts go, it is not impossible to regard the Caytoniales as forms derived from a Pteridosperm complex, by the development of the closed, protecting, carpel wall, either from a cupule-like structure of the type seen in *Gnetopsis*, or in a manner to which the known Pteridosperms furnish no clue.

(*b*) *Bennettitales.*—The possibility of a phyletic relationship between the Bennettitales and the Angiosperms has been so widely discussed that it is desirable to ascertain

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[*] OLIVER and SALISBURY (1911), pp. 7–35.

[†] *Idem*, p. 14.

whether any similarity can be traced between the Caytoniales and this important group of Mesozoic plants.

We know nothing of the stems of the Caytoniales, while the leaves of the *Sagenopteris* type seem very remote from the regular cycadean leaf-form which characterised the Bennettitalean group. The pinnæ of *Dictyozamites* have indeed a reticulate venation, but this character appears in several totally unrelated classes of plants and cannot be regarded as significant.

The most constant and characteristic feature of the Bennettitales is the ovulate strobilus, and this permits of no comparison with the fruit structures described above. Neither do the microsporophylls and synangia suggest any closer comparisons with the anther-bearing structures named *Antholithus Arberi*. Though the groups of anthers were arranged in a pinnate manner on a central axis, the individual anthers were vastly different from even the simpler synangia of the Williamsonieæ, with their many compartments packed with microspores.

The only feature in which a valid comparison seems possible is the structure of the testa, and here the degree of similarity is about the same as can be traced between the Caytoniales and the Pteridosperms and the Gnetales.

Dr. MARIE STOPES has given us recently a very complete account of the testa structure of *Bennettites albianus*,* and we have also the accounts given by LIGNIER† for *B. Morierei*, and the description of the testas of some species of Cycadeoidea by WIELAND.‡ From the work of these authors we see that the sequence of tissues and their characters in the Bennettitalean testa was almost identical with those in the testa of *Caytonia*.

The outer "blow-off" layer of *Caytonia* seems to find a parallel in the layer which WIELAND describes under the same name, but which Dr. STOPES more cautiously calls the "deliquescent" layer. The palisade layer corresponds to the stone layer of *B. albanius*, and the other forms, while the next layer, the fibres, agrees with the middle stony or fibrous layer in the English and French specimens, and probably to the inner flesh of WIELAND. Within the fibres in both groups there seems to have existed a layer of thin-walled cells which Dr. STOPES was unable to regard as separate from the rest of the testa, but which does seem separable in *Gristhorpia*, and which is here regarded, perhaps somewhat rashly, as the inner integument.

Another point of general similarity is the absence of an integumentary vascular system in both classes of seeds. But this is a character of physiological rather than of phyletic significance. The seeds of the Pteridosperms and of the Gnetales which possess such a vascular system are exposed, while the seeds of the Bennettitales were protected against transpiration by the interseminal scales almost as effectively as were those of the Caytoniales by the closure of the carpel.

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* STOPES (1918), p. 403.

† LIGNIER (1894), p. 43.

‡ WIELAND (1916), p. 138.

The comparison of testal structure is not, however, complete. According to the authors cited above, the Bennettitalean seeds were radiospermic with four or five ribs of larger stony cells in the upper part of the testa. These ribs appear to be absent from the mature seeds of the Caytoniales, which may have been platyspermic. The structure of the micropyle was also different; the long tube characteristic of the Bennettitales is here wanting. In *Caytonia* the flange-like extension of the cells lining the micropylar tube over the apical part of the testa is unlike anything which has been described in *Bennettites* or *Cycadeoidea*. WIELAND says that "the extreme end of the *Cycadeoidea* inner integument never quite extends beyond the outer integument, or comes to form a final capping of the micropylar tube as in *Gnetum gnemon*."* It is not easy to make out exactly what he wishes to imply, as this seems to be the only reference in his discussion to the presence of an inner integument in *Cycadeoidea*.

But even though the similarities in the testal structure may be close, the way in which the ovules of the Caytoniales were produced, pollinated and protected is so remote from anything seen in the Bennettitales as to preclude any connection, save through very distant ancestors. If we are entitled to regard the Caytoniales as anywhere near the main line of evolution of the modern flowering plants, or even as remotely connected with this line, we must regard the Bennettitales as a group which is still more remote. And if their bisexual strobilus superficially resembles a Ranalian flower, it must have arisen by an independent though parallel line of evolution.

(*c*) *Gnetales*.—Many authors have attempted to trace some connection between the Angiosperms and the Gnetales† on the ground of their vascular anatomy and their embryo-sac structure. The view most favoured is that the Gnetales and the Angiosperms have descended from a common stock such as the hypothetical Mesozoic group called by ARBER and PARKIN the Hemiangiosperms.‡

BERRY has suggested that the problematical Cretaceous leaves, *Ficophyllum*, *Rogersia* and *Protœophyllum*, with which the leaves of *Sagenopteris* were compared above, may be early representatives of the Gnetales.§ We may then enquire as to what extent the Caytoniales may be compared with this group.

In such a comparison we again find some points of similarity combined with many wide differences. It seems almost impossible to trace any homologies between the infructescences described above and the female inflorescences of the Gnetales. The male inflorescences are likewise very different, though the antherophores of *Ephedra* possess some similarities with the male flowers described above. According to THODAY and BERRIDGE,|| the antherophores of *B. fragilis* are foliar in nature, and show a circinate vernation; in several species they broaden out to form a fairly wide lamina when

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* WIELAND (1916), p. 145.

† *Cf.* PEARSON (1909), p. 385.

‡ *Cf.* ARBER and PARKIN (1908).

§ BERRY (1911), p. 497.

|| THODAY and BERRIDGE (1912), p. 974.

mature. In *E. distachya* the antherophore is clearly bifid and each half bears four synangia on one surface near its apex. This arrangement of synangia is perhaps more similar to the manner in which the anthers of *Antholithus Arberi* are produced than to any other seen in recent plants.

The manner in which the Gnetalean ovules are produced and protected is far different from that seen in the Caytoniales, but in the details of the structure of the integuments there are again certain similarities. The typical Gnetalean ovule seems to possess a nucellus surrounded by two integuments, the outer complex in structure, the inner more delicate and prolonged to form the micropylar tube. The curious structure of the micropyle of *Caytonia* is not unlike that seen in *Gnetum africanum** where the inner integument lines the micropyle and forms at the summit a flange overlapping the outer integument or middle covering of the seed. In both cases the canal of the micropyle is cutinised. The outer integument of *Caytonia* is also comparable with the middle covering of the seed of *G. africanum* in its complex structure, though it contains no vascular bundles. In both three layers are present and the structure of the two inner layers is identical, but the outer layer of the *Gnetum* seed is composed of several rows of isodiametric cells with vascular bundles, while the "blow-off" layer of *Caytonia* is a delicate layer one cell thick.

What significance should be attached to such resemblances? It should be noted that they are similar to those already recorded for the Pteridosperm *Conostoma* and for *Bennettites*, but here we have a closer similarity in the structure of the micropylar tube. Such facts seem to point rather to common ancestry and parallel evolution than to close relationship. The cutinisation of the micropylar tube found in *Caytonia*, *Bennettites* and *Gnetum* is probably the outcome of a similar physiological mechanism in the three genera. The comparison of the antherophores of *Ephedra* may be a more important point, and again suggests the possibility of the derivation of the Caytoniales and Gnetales from a common Pteridospermous ancestor somewhat like *Crossotheca*.

The Caytoniales cannot be regarded as connected with the hypothetical Hemiangiosperms† with open carpels, from which, on ARBER and PARKIN's view, the Gnetales and Angiosperms were considered to have sprung. They were non-strobilate, the microsporangia and megasporangia do not seem to have been produced in close proximity and may, indeed, have grown on separate plants.

(*d*) *Angiosperms.*—It is not my intention to attempt a detailed comparison of the Caytoniales with the modern Angiosperms. We may, however, notice a few points in this connection. At the outset it may be observed that the reproductive organs described above are in their general features very unlike anything known to me in the modern group of the flowering plants. There is no approach to a typical flower either in the male or female parts, but, on the other hand, we see the two essential parts of the Angiosperm flower closely foreshadowed, the closed carpel with a stigma and the four-lobed anther.

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* THODAY (1911), p. 1112.

† ARBER and PARKIN (1907).

In no previously described fossil of Mesozoic age have reproductive parts been found which correspond so closely with those of the Angiosperms. In theory it is easy to postulate the production of a closed Angiosperm carpel from a megasporophyll with ovules borne on the margins, but there is no evidence derived from fossils to show when or how the closure took place which involved such a great change in the life history of the plant. In like manner the Angiosperm stamen is far removed from any synangium seen in the Bennettitales or Pteridosperms.

Thus while the Caytoniales seem quite distinct from the existing groups of Angiosperms, and we cannot regard them as the ancestors of many, if any, of the present-day forms, we are bound to regard them as closely allied to the forms from which the modern flowering plants sprang.

The well-known investigations of NATHORST and others have shown that among the Bennettitales forms existed in which the microspores were produced in synangia borne on bi- or tri-pinnate structures (*Williamsonia spectabilis*), but other closely allied genera showed a reduction of the microsporophylls to a simple structure bearing about three or four synangia on either side (*Williamsoniella*), while a third form shows a simple ring of apparently sessile synangia with no trace of the pinnate foliar structure (*Wielandiella*).* There is no reason to suppose that a series of changes which has taken place in one group could not take place in a contemporary group, and that in other (unknown) forms allied to the Caytoniales the pinnate foliar structure bearing the carpels and anthers may not have been so reduced that the carpels and anthers were borne singly on the axis.

It is unfortunate that at present we know so little as to the method in which the micro- and mega-sporophylls were borne on the stems in the Caytoniales, but it seems certain that they were not produced in close strobili or crowded together.

It involves, however, no great morphological assumptions to suppose that the sporophylls may have become crowded together into a strobilus by the condensation of the axis in some forms, and that at a very early period in the history of the Angiosperms we may have had unisexual male strobili and female strobili in some families, and bisexual strobili in others. It is possible, too, that the aggregation of sporophylls varied from a mere ring of a few members to a large and compact strobilus of many members. If such a theory were correct we might expect to find among the recent Angiosperms occasional examples in which traces of the former pinnate nature of the micro- and mega-sporophylls were still found. The branched stamens of *Ricinus* and *Maprounea* might be regarded as such examples, while the parts of the complex catkins of the Fagales might, in some cases at least, be open to a similar interpretation. The female catkin scale of *Betula* might well be a megasporophyll bearing three carpels derived by condensation from a pinnate structure.

It seems to me that once this group of plants had evolved the carpel and the stamen—the units on which cross pollinating influences could work—it was bound to evolve various types of floral structure in which the essential units were arranged in different

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* *See* THOMAS (1915), p. 138.

ways on the axis which bore them. The fact that the carpels and stamens of the Caytoniales were arranged very differently from those of any modern Angiosperm does not seem to be of such fundamental importance as to separate them completely from the group of plants now known as the Angiosperms.

The form of the fruits of the Caytoniales bears some slight resemblance to the ripe fruits of some genera of the Menispermaceæ. Here the development of the fruit is often accompanied by a great enlargement of the dorsal side, while the ventral side elongates but little. In this way the stigma, which is at first produced at one side of the apex, comes to occupy a position close to the stalk of the fruit. The figures given by DIELS of the fruits of *Stephania abyssinica* (Dill et Rich.) WALP,[*] and of *Syrrheonema fasciculatum* MIERS[†] may be compared with the figures given above (text-figs. 3, 5). This similarity may be casual, but it is worthy of note, for the presence of such a peculiar feature in the Menispermaceæ seems without biological significance and may be a relic of an ancestral character.

The same type of development is seen also in the fruits of *Tetracentron sinense* (OLIV.), a member of the Magnoliaceæ, where the styles of the carpels become dorsal and finally basal during the enlargement of the developing ovary.[‡] In this plant each carpel contains about four ovules and is, therefore, more comparable with the carpels of *Gristhorpia* and *Caytonia.*

It is obviously impossible to suggest any affinity between the Caytoniales and the Menispermaceæ or Magnoliaceæ, but at the same time the occurrence of such a curious feature in two families of the Angiosperms, which have some claim to be considered as antique, gives us further reason for connecting the Caytoniales with the recent Dicotyledons.

We have referred above to the similarity in seed structure between *Caytonia* and the Gnetales, Bennettitales and the Pteridosperms. We should here notice that the structure of the testa of *Gristhorpia* was much simpler, and was lacking in fibrous elements. It seems possible that in both my genera there were two integuments, and we have here a point of comparison with the Angiosperm seed. It may further be noticed that many Angiosperm seeds give a similar appearance to that shown by *Caytonia* and *Gristhorpia* when macerated in SCHULTZ's solution. The megaspore membrane remains as the most distinct feature, while the outer integument may be lightly cutinised and this may extend to the micropyle.

But the main points of comparison of the Caytoniales with the Angiosperms must be: first the shape of the stamens with their four angles, four loculi and longitudinal dehiscence along the groove between the ridges; secondly, the fact that the ovules were borne inside closed carpels with a distinct and physiologically specialised stigma, that there were many orthotropous ovules, sometimes arranged in two

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[*] DIELS (1910), p. 269, fig. 89 M.N.

[†] DIELS (1910), p. 90, fig. 32 J.K.

[‡] OLIVER (1889), Pl. 1892.

rows, each probably having two integuments and other features in common with the Angiospermous ovule.

Such essential features link the Caytoniales closely with modern Angiosperms.

SYSTEMATIC POSITION OF THE CAYTONIALES.

The plants described in this paper belong to a type which appears very distinct from any genera of living plants known to me. Dr. A. B. RENDLE, of the British Museum, has been so kind as to look at some of my figures, and considers that the carpels and fruits cannot be closely compared with those of any modern Angiosperm. We must therefore consider the position of these forms in the classification of fossil and modern plants.

We are especially fortunate in having male and female reproductive structures as well as mature fruits and seeds, but the matter is not a simple one. It is, of course, certain that the Caytoniales belong to the division Embryophyta siphonogama or Phanerogamæ. The way in which the carpels are produced on a pinnate dorsiventral structure, together with the structures of the integument or testa in Caytonia, indicates a possible near relationship with the Pteridospermæ, but the closed carpels with pollen grains deposited on a stigma remove them from this group. The closed carpel and stigma seem to leave little doubt that the Caytoniales cannot be regarded as Gymnosperms in spite of the similarities in seed structure with the Gnetales and Bennettitales; we must regard them as *Angiosperms.*

Beyond this it is difficult, if not impossible, to proceed further. We know, unfortunately, nothing about the structure of the embryo, nor do we know what were the anatomical features of the stems. The leaves, if my views are correct, were reticulatedly veined, but the arguments advanced for the original connection of Sagenopteris are not beyond dispute. From the way in which the remains are found, I imagine that the original plants were probably trees or shrubs, but I have no sound basis for this supposition. The characters of the inflorescences seem to remove them from the immediate connection with any modern group, either of Monocotyledons or Dicotyledons, and it is possible that at the time when they existed these classes had not yet become distinct.

The differences between the Caytoniales and the modern Angiosperms are so considerable that the view may well be put forward that the former had no real connection with our modern Angiosperms. That they represent an extinct class of plants which had arisen from the Pteridospermæ along a line in which some such form as *Gnetopsis* became completely enclosed in a cupule-like covering, which ultimately formed the structure described above as the carpel wall, and also developed siphonogamy. It may be held that the Caytoniales represent one of the last members of this series, which soon became extinct, while the modern Angiosperms were evolving along other lines from different ancestors. Such a view is possible, but is somewhat gratuitous.

The closed carpel of *Caytonia* with two rows of ovules borne within on the dorsal side is a feature which is found in many recent Angiosperms, but does not appear in any other group. The formation of a stigma from the carpel wall with a papillate receptive surface is a typically Angiospermous feature. The method in which the *Gristhorpia* stamens were produced is reminiscent of *Crossotheca*, but the form and structure—so far as it can be ascertained—of each stamen is again highly suggestive of an Angiosperm, and a comparison with *Ricinus* is possible. If we reject the idea that the Caytoniales occupy a position among the earliest Angiosperms, because of the form of the inflorescence and the apparent complete absence of perianth leaves, we shall have to disregard features of major importance in favour of points of minor importance. The closed carpels and the stamen structure show that the Caytoniales stand much nearer to the direct line of Angiosperm descent than any known plant of the Bennettitalean type, in spite of the strobilar form of the "flower" and the perianth of that group.

But it cannot be denied that the Caytoniales are far removed from most modern Angiospermous types. If my deductions from the cuticular structure of the axis of both the male and female parts are correct, and these dorsiventral structures do represent reduced or modified leaves, we are a long way from any modern angiosperm floral structure, but we do not know how such megasporophylls were arranged on the original stem.

I do not propose to discuss this subject further, as my knowledge of the modern angiosperms is insufficient to enable me to make any contribution of value on the morphology of the Angiosperm flower as affected by the discovery of the Caytoniales. I must leave this to others. But I may suggest that the evolution of the closed carpel was an event of immense significance in the development of the plant world. It provided a means of pollination which especially increased the chances of cross-fertilisation and which would probably tend to the development of numberless forms. It provided a means of seed dispersal which might well have been of still greater importance in increasing the chance of the establishment of mutations. It is not without significance that the Caytoniales, with their fleshy fruits, are almost contemporary with the appearance of the first bird-like animals (*Archæopterix*), which may, perhaps, have found in these fruits a tasty diet. If so, the hard seeds of *Caytonia* would probably be indigestible, and would pass uninjured through the alimentary canal of the bird.

But we ought also to notice that there is no reason to suppose that the Caytoniales were the only Angiosperms in the world at the time. The leaf described by Prof. SEWARD from the Stonesfield Slate indicates that other types were probably present, and such types may have been nearer to the main line of Angiosperm descent.

The Caytoniales almost certainly grew in the swampy lagoons of an estuary, and may, even in the Jurassic period, have been a somewhat archaic or aberrant type. At the present day, if we take a vegetation type developed under special edaphic conditions, it may well contain samples of the main plant types of the world, but not always typical samples. Thus we have in the Indo-Malayan estuaries a short-stemmed Palm *Nipa*, which is not altogether typical of the modern palms and is known to be an ancient type. I should like to suggest that, while in the Caytoniales we have the only Angiospermous plants yet known at all completely from the Jurassic age, they may only be a bad sample of the Angiosperm vegetation of the period. The more typical Angiosperms of the period may well have flourished on the dry land far from a locality in which their leaves, flowers, or fruit had any chance of being buried in mud or preserved as fossils, for even the tissues of Caytoniales are very delicate.

It is highly probable that there were contemporary Angiosperms in which the flowers had already evolved a structure which was nearer to that of the modern flower. Dr. MARIE STOPES* has shown that woody dicotyledonous stems of various types existed in Aptian times, if not at an earlier date. Various types of Angiosperm leaves have been found in the Neocomian beds of Portugal and North America, while the abundance of types in Europe and America at a later date is well known. All these forms must have sprung from ancestors living during the Jurassic period.

Botanists who have speculated upon the origin of the Angiosperms have often been allowed some licence, and perhaps this may be extended to the author on this occasion. The question naturally arises, what was the origin of the Caytoniales ? We have seen that there is some evidence of their existence in the Upper Triassic (Rhætic) times, but one wonders whether they can be connected with any group of plants found in the Palæozoic ; their affinities with the types known from the Carboniferous rocks of the Northern Hemisphere seem slight ; they may I believe be more closely connected with the plants of the Glossopteris flora.

There seems no reason to doubt that the Caytoniales descended from Pteridosperm ancestors. Both the male and female inflorescences point to the same conclusion. The European Palæozoic *Gnetopsis* is perhaps the nearest known Pteridosperm as regards the structure of the carpel. But if the leaves of the Caytoniales were really of the *Sagenopteris* type, we cannot easily find a closely comparable form in the Northern Palæozoic flora, and instead we must go to the dominant plant type of Gondwanaland—*Glossopteris*.

The similarity of form and nervation between *Glossopteris* and *Sagenopteris* is indicated by the fact that some earlier authors placed leaves clearly referable to the latter in the former genus. There is, in fact, little to distinguish leaflets of *Sagenopteris* from the leaves of *Glossopteris*. Though the leaves described above are generally compound structures, some forms were simple, *e.g.*, the rounded forms of var. *cuneata*, and while, on the other hand, the specimen from the Transvaal, figured by Prof. SEWARD† as leaves attached to a rhizome, might possibly be of the nature of a compound leaf with palmately arranged leaflets. Thus the only important distinction in leaf form is not to be relied upon. External form, however, provides poor evidence of relationship.

We do not yet know in what group of the plant kingdom *Glossopteris* should be placed.

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* STOPES (1912).

† SEWARD (1910), p. 504, fig. 339.

ARBER[*] discovered sporangia-like objects on some of the scale fronds, but was unable to isolate spores from them. These structures may be the microsporangia, and it is quite probable that *Glossopteris* was a Pteridosperm.[†]

It may be significant that while in many Rhætic floras *Sagenopteris* is present, it is absent in the fossil flora of TONKIN[‡] where *Glossopteris* is present. Likewise in the Liassic flora of Mexico a form identified as *Glossopteris* is present, and *Sagenopteris* is absent.[§]

There are two great problems with regard to the evolution of the Angiosperms. First, that when they definitely appear in the Cretaceous rocks we find a large number of Angiosperm types already in existence. Second, that on their appearance they are seen to be distributed widely over all the world.

The suggested hypothesis that the Angiosperms sprang from plants of the Glossopteris type, which covered a considerable area of the earth in Permo-Carboniferous times, has therefore some features of interest and is worth an effort to prove or disprove it.

Whatever the value of such a purely speculative suggestion, the evidence brought forward in this paper shows that in early Jurassic times a race of plants existed which had some of the primitive characters of the Pteridosperms, and at the same time possessed some of the most distinctive characters of the Angiosperms. These plants have thus some claim to be regarded as suggesting a solution of one of the greatest historical problems of plant evolution.

SUMMARY.

The Caytoniales constitute a new class of angiospermous plants which has been founded on the remains of megasporophylls, fruits, seeds and microsporophylls bearing stamens.

The megasporophylls, carpels, fruits and seeds have been separated into two groups which are regarded as belonging to distinct genera, each genus being represented by one species. These have been named *Gristhorpia Nathorsti* and *Caytonia Sewardi*. The microsporophylls have been identified with specimens already described by Prof. SEWARD, and are called *Antholithus Arberi*.

The material examined consists of a large number of specimens which have been collected by the author in the Gristhorpe plant-bed in Cayton Bay, near Scarborough, Yorkshire. This bed belongs to the Middle Estuarine Series of rocks, and is of Middle Jurassic age.

The specimens are exceptionally well preserved, and in addition to the examination of their surface features, much has been discovered as to their structure by maceration methods, and also by the use of a new technique which has enabled the structure of thin sections to be made out.

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[*] ARBER (1905), p. 324.

[†] While this paper was in the press I discovered groups of structures similar to ARBER'S sporangia, associated with seeds and leaves of *Glossopteris*, in material collected in Natal by Mr. Mogg.

[‡] ZEILLER (1903), pp. 84, 297.

[§] WIELAND (1916), Lam. 17, fig. 2; 46, fig. 3.

Both *Gristhorpia* and *Caytonia* seem to have possessed pinnate megasporophylls with a carpel formed from the tip of each pinna. The stigmas had the form of flaps or semicircular flanges at the bases of the carpels near the stalks. Probably the whole structure had a pendulous habit of growth. The epidermal structure of the axis of the megasporophyll shows a marked dorsiventrality.

Gristhorpia had a large stigma which is strongly cutinised in the fruit stage. On the stigmas of some young specimens the remains of very characteristic pollen grains have been found. The fruits became fleshy and contained eight or more seeds. There are indications of the original presence of a large number of ovules with parietal placentation, most of which were not fertilised. Some points in the structure of the seeds can be made out by the maceration of isolated specimens. There are indications of the presence of two integuments, while the megaspore membrane with an apical projection, and the lining of the micropyle with cutinised cells are noteworthy features.

The seeds and fruits of *Caytonia* had a harder texture, and it is possible to obtain sections showing the structure of the seeds and fruit wall. The stigma was smaller but cutinised also. The integuments had a complex structure. Outside was an evanescent " blow-off " layer, next a stony palisade layer and then a fibrous layer. There are indications of a parenchymatous tissue next to the megaspore membrane, which is continuous with the rounded cells lining the micropyle, and which is regarded as the inner integument. The seeds were probably arranged in two rows on the wall of the fruit, and seven or eight reached maturity. Isolated seeds are often found.

The male inflorescences had the form of pinnate microsporophylls and the pinnæ are often forked or again pinnately divided. Groups of four-lobed anthers were produced at their tips, which were very similar to the anthers of the modern flowering plants. From these anthers characteristic winged pollen grains have been extracted which are identical with those found on the stigmas of *Gristhorpia*.

No typical dicotyledonous leaves are found in the plant beds of the Estuarine Series of Yorkshire, but the remains of the Caytoniales are constantly associated with leaves of the type long known as *Sagenopteris*. Out of 152 hand-specimens showing remains referable to the Caytoniales, 133 show leaves of *Sagenopteris* on the same face, and in only 19 specimens are leaves of this type absent. There are considerable similarities in the form and cutinisation of the epidermal cells between the petioles of *Sagenopteris* and the axes of the megasporophylls. The venation of *Sagenopteris* is also similar to the primary venation of many dicotyledonous leaves. It is probable that the plants of the Caytoniales bore leaves of the Sagenopteris type.

The cuticular structure of the lamina and petiole of specimens included in the old form *Sagenopteris Phillipsi* (Brongn.) shows some indications that the leaves of more than one type of plant may have been included in this form-species.

The comparison of the Caytoniales with previously described fossils of a similar form is rendered very difficult by reason of the paucity of detailed information about the latter. A number of specimens have already been described which are somewhat similar in external appearance, and which may be suspected of having had affinities with the new class. Among these may be mentioned *Strobilites Milleri* and *Hydropterangium marsilioides*, which have also been found associated with leaves of the Sagenopteris type.

A comparison of the Caytoniales with other seed plants seems to indicate that affinities may be traced with the Pteridosperms, Bennettitales, Gnetales and modern Angiosperms.

Resemblances with the Pteridosperms may be found in the general form of the mega- and micro-sporophylls, while some of the details of seed structure in *Caytonia* are comparable with those seen in the Conostoma group.

The comparison with the Bennettitales and the Gnetales is confined mainly to the structure of the integuments of the seed. The form and cutinisation of the micropyle in the seeds of *Caytonia* is more like that seen in *Gnetum* than in any other seed.

The Caytoniales possess two of the features most characteristic of the modern flowering plants, viz., the closed carpel with a stigma, and the anther with four longitudinal lobes. On this account it seems permissible to group them with the modern Angiospermæ, though they do not seem to resemble any modern family. It is possible that they belong to a line of evolution which was quite distinct from that which gave rise to the modern Dicotyledons and Monocotyledons, and represent a parallel series of forms now completely extinct.

No attempt has been made to institute a close comparison with the multitudinous forms of carpel, fruit, seed and stamen structure found in the Angiospermæ of to-day.

The Caytoniales seem to occupy a position between the Palæozoic Pteridosperms and the recent Angiosperms, and thus they suggest a possible solution for one of the great outstanding problems of evolution.

ACKNOWLEDGMENTS.

This work is the outcome of the re-investigation of the Jurassic flora of Yorkshire which was commenced some years ago at the suggestion of Prof. A. C. SEWARD, to whom I am greatly indebted for constant advice, assistance and encouragement.

The collection of many of the specimens was greatly facilitated by a grant from the British Association for the Advancement of Science.

A large number of friends have kindly given information on various points which have been encountered, while my wife has assisted in the preparation of the results for publication. To all of these my best thanks are due.

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DESCRIPTIONS OF PLATES 11-15.

(Photographs by the Author.)

PLATE 11.—*Gristhorpia Nathorsti* gen. et sp. nov.

Fig. 1.—Main axis showing a young fruit attached to it, and the scars (*s*) of two fruits which have become detached. A detached older fruit is seen above. × 2·5.

Fig. 2.—Part of a macerated fruit showing epidermis of the fruit wall and remains of membranes from the enclosed seeds (*m*). × 75.

Fig. 3.—Macerated specimen of an old fruit which has burst open at the top. The dark hump near the stalk on the left is the remains of the stigma. × 6.

Fig. 4.—One of the youngest specimens showing the main axis with a row of stalked carpels on one side. (The other row is buried in the matrix.) The preparation showing pollen grains on the stigma (Pl. 14, fig. 42) was obtained from one of these carpels. × 2·5.

Fig. 5.—Infructescence showing two rows of fruits. The central axis is buried in the matrix and is only exposed in one place in the centre. Nat. size.

Fig. 6.—Two young fruits showing their pedicels and the stigmatic flaps near their bases. × 2·5.

Fig. 7.—Young fruit detached from the matrix showing longitudinal wrinkling, stigma and pedicel. × 5.

Fig. 8.—Old fruit burst open with isolated seed lying near. × 2.

Fig. 9.—Old fruit showing apical fissure. × 2.

Fig. 10.—Longitudinal section of stigma of specimen shown in text-fig. 3, showing the inverted funnel shaped opening lined with lighter, cutinised cells which extend upwards into the centre of the fruit, thinning out again into two points. The substance of the fruit is irregularly fractured above. × 54.

Fig. 11.—Apical part of macerated seed shown in fig. 12. Note dark megaspore membrane with plinth-like flange at the top; above this are the cutinised cells lining the micropyle. The external cells of the inner integument are papillate. *Cf.* text-fig. 4. × 185.

Fig. 12.—Complete macerated seed, showing in the centre the megaspore membrane, with the micropyle at its apex. The thin line surrounding the seed is the remains of the inner wall of the blow-off layer, and the space below it shows the position of the palisade layer. Some cells of the parenchymatous layer, which possibly corresponds to the inner integument, are seen near the micropyle. × 28.

Fig. 13.—Remains of the seed membranes extracted from a closed fruit. They were somewhat broken up in extraction, but the characteristic cells lining the micropyle are seen at *m*. Remains of the fruit wall are seen at *f*. × 32.

PLATE 12.—*Caytonia Sewardi* gen. et sp. nov.

Fig. 14.—Specimen showing the remains of two infructescences, with leaves of *Sagenopteris, Pagiophyllum* and *Taeniopteris*. Nat. size.

Fig. 15.—Magnified view of the upper infructescence shown in fig. 14. The fruits are lying on top of the axis, which is only seen near the base. × 2·5.

Fig. 16.—Part of an infructescence showing its attachment to a larger branch, also isolated fruits in which the outlines of seeds can be made out. No perianth scars can be found on the axis or on the branch. × 2·5.

Fig. 17.—Single fruit embedded in the matrix showing flange-like stigma (*s*) at the base. The pedicel is only just visible. × 9.

Fig. 18.—Longitudinal section of a fruit passing through the stigma somewhat tangentially. The pedicel is seen below and the stigmatic flange at *s*. Note the cutinised cells lining the stigma and spreading inwards. *Cf.* with fig. 20. This section was not chemically treated after cutting and no structure is seen in the upper part. × 109.

Fig. 19.—Section of a fruit (series Z) cleared with Schultz's fluid and dilute ammonia. Part of the structure of four seeds is shown. The thick cuticle of the fruit wall is seen at *w*; the remains of a fibrous layer at *f* and in other places; the teeth on the outside of the seeds left by the solution of the blow-off layer at *t*. The section at *m* passes through a micropyle. A megaspore membrane is seen at *e*. × 106.

Fig. 20.—Median longitudinal section through a stigma compressed on the side of an isolated fruit. The stigmatic opening lined with cutinised cells is seen, with part of the pedicel above and the stigmatic flap below. Note the extension of the cutinised cells into the fruit. Just below a seed is seen in which the structure is visible. The megaspore membrane *e* is surrounded by darker cells, the fibres *f*, outside which is the palisade layer *p*. The seed is close up against the fruit wall at the point where the stalk enters, which seems to exclude the possibility of the occurrence of an axile placenta. Section cleared with hydrochloric acid and potassium chlorate followed by sodium sulphite. × 109.

Fig. 21.—Isolated seeds in a hand specimen in which they occur in large numbers. × 4.

Fig. 22.—Group of separate fruits showing clearly the enclosed seeds. Nat. size.

Fig. 23.—Macerated fruit. Only the cuticle of the fruit wall remains with the remains of seeds (not shown) inside. The dark piece at *s* is the remains of the stigma; the pedicel was detached from the point below the stigma, where a small gap is seen. × 5.

Fig. 23A.—Isolated fruit detached from the matrix, similar to the examples which were cut into sections. The stigma occurs at *s*, but is not clearly shown. × 3.

Fig. 24.—Isolated detached fruit from which the wall had been broken away showing seeds inside. × 3.

PLATE 13.—*Caytonia Sewardi* gen. et sp. nov.

Fig. 25.—Section through a fruit after treatment with Schultz's fluid followed by alcohol and formalin. The middle lamellæ of the cells are now visible. In the upper part a seed is seen in longitudinal section. In the lower part another seed has been cut more transversely. *b*. Blow-off layer which is only seen near the fruit wall. *e*. Megaspore membranes (and remains of embryo ?) *p*. Palisade layer. *f*. Fibres in longitudinal section. *f* ′. Fibres in transverse section. × 108.

Fig. 26.—Apical part of an isolated seed after prolonged maceration and clearing, showing the megaspore membrane and the cutinised cells of the micropyle. The outer cuticle of the seed is just visible round the flange of micropylar cells at the apex. *Cf.* text-fig. 9. × 75.

Fig. 27.—Isolated seed which has been macerated and partly cleared, showing the remains of the fibres round the megaspore membrane. A dark spot marks the point of attachment, but the micropyle at the upper end is not clearly seen. × 32.

Fig. 28.—Tangential section through the wall of the fruit (after treatment by sodium sulphite method). Note the thick cuticle and the remains of large irregular cells which may have been fleshy during life. × 200.

Fig. 29.—Part of the longitudinal section through the fruit shown in fig. 32 (series Z, after treatment by alcoholic ammonia method). Parts of four seeds are seen. The seeds are separated by a cutinised membrane *m*, no trace of a blow-off layer remaining. The fibrous layers *f* are clearly seen and the palisade layer *p* is faintly visible. In the centre of each seed the megaspore membrane *e* appears, with little or no trace of a contained embryo. × 126.

Fig. 30.—Section of a fruit (series O) treated in the same way as that shown in fig. 25. Parts of five seeds are seen. The blow-off layer is only seen in one place. Lettered as in fig. 25. × 108.

Fig. 31.—Part of a section through a seed after somewhat prolonged clearing with alcoholic ammonia, showing the remains of the outer cuticle of the seed coats (*m*) and spicule-like remains of fibres *f* on both sides of the megaspore membrane *e*. × 220.

Fig. 32.—Complete longitudinal section of a fruit showing seven seeds within. The stigma was at the bottom of the section, and the club-shaped projection at the top was formed from the fruit wall. The seeds occupy similar positions to those shown in text-fig. 8. The central portion, more highly magnified, is shown in fig. 29. × 30.

PLATE 14.—*Antholithus Arberi* sp. nov.

Fig. 33.—Largest specimen showing the central axis and side branches to some of which anthers, *a*, are still attached. × 3.

Fig. 34.—Cuticle preparation from the main axis showing the difference in the size and shape of the cells on the two sides. The right-hand portion of the preparation comes from one side, the left-hand portion from the opposite face. × 50.

Fig. 35.—Specimen showing the scattered remains of anthers and the stalks on which they were borne. × 3.

Fig. 36.—*a*. Part of a main axis with short side branch and two anthers, showing their four-lobed form. *b*. Fragments of anthers in which the lobes have become separated. *c*. Single anther and branch bearing forked appendages on which the anthers were borne. × 3.

Fig. 37.—Part of main axis bearing side branches (pinnæ) detached from the rock; the forking of one of the side branches is shown. × 5.

Fig. 38.—A single pollen grain, extracted from the interior of an anther, showing the two lateral wings with granular surface markings. × 600.

Fig. 39.—Tip of an anther which has been macerated, showing three of the four lobes still united at their tips; the elongated epidermal cells can just be made out. × 30.

Fig. 40.—Mass of winged pollen grains extracted from a macerated anther. × 220.

Gristhorpia Nathorsti gen. et sp. nov.

Fig. 41.—Cuticle preparation from part of the main axis of a young infructescence (sporophyll), showing the difference in the thickening and size of the epidermal cells on the two sides. The lateral margin of the axis is represented by the dark mass in the centre of the preparation. *Cf.* text-fig. 11, A.B. × 40.

Fig. 42.—Cuticle preparation of part of the stigma of a carpel or young fruit which shows at *p* a number of winged pollen grains identical with that shown in fig. 38. × 230.

PLATE 15.—*Gristhorpia Nathorsti* gen. et sp. nov.

Fig. 43.—Part of a squashed fruit with seeds and small black structures (aborted ovules ?) which appear to have been extruded from it. × 4.

Fig. 44.—Group of seeds and small rounded or oval bodies thought to be aborted ovules, mounted in Canada Balsam and freed from matrix by Mr. J. WALTON'S method. This preparation was made from the counterpart of the specimen shown in fig. 43, and was photographed by transmitted light. × 4.

Fig. 45.—Cuticle preparation of part of the main axis of a young infructescence near a pedicel, showing the difference in the epidermal structure on the upper and lower sides. *Cf.* Pl. 14, fig. 41, and text-fig. 11. × 35.

Fig. 46.—Two young carpels probably from the tip of a megasporophyll. The right hand specimen shows the stigma at the side of the stalk. *Cf.* fig. 47. × 4.

Fig. 47.—The right hand carpel of fig. 46 more highly magnified. It suggests the formation of the carpel from the recurved lamina of the megasporophyll pinna, and the production of the stigma where the tip of the lamina touches the pedicel. *Cf.* text-fig. 2. × 20.

Caytonia Sewardi gen. et sp. nov.

Fig. 48.—Cuticle preparation from main axis of an infructescence (megasporophyll), showing the great difference in the cuticle structure of the two sides and the rounded spots which may be the bases of hairs such as are found on the leaves of *Sagenopteris*. The larger cells of the upper side, shown on the right of the photograph, possess fine projecting points which are not clearly seen at this magnification. *Cf.* text-fig. 12, A, B. × 50.

Sagenopteris Phillipsi (Brongn.).

Fig. 49.—Cuticle preparation from a *Sagenopteris* petiole in specimen CA 10, which was almost indentical in structure with that of a *Caytonia* axis lying near it. The difference in the cells of the two sides are here less pronounced, but the projecting points on the cell walls can be made out. × 65.

Fig. 50.—A typical leaf with four lanceolate leaflets attached to a petiole. Some detached leaflets are also seen. The leaflets have midribs in their lower portions, which die out towards the apex. Cuticle preparations made from petioles of similar specimens have the structure shown in text-fig. 11, C and D. × 3/4.

Fig. 51.—An example of the smaller type of leaf possibly referable to *S. Phillipsi* var. *cuneata*. The three leaflets are small and ovate, with a very short midrib, and the remains of the lamina are very delicate. The structure of the petiole epidermis in this form is similar to that of the axis of *Caytonia Sewardi*. Nat. size.

Fig. 52.—Example of a simple Sagenopteris leaf with no lateral pinnæ, at the apex of a petiole. The petiolar material had been removed for the study of its cuticle. It has no noticeable midrib. Nat. size.

Fig. 53.—Part of a leaflet of the type shown in fig. 50 detached from the matrix and photographed by transmitted light to show the venation. × 4·5.

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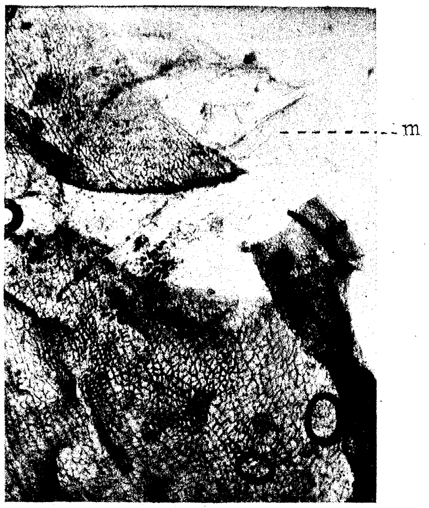

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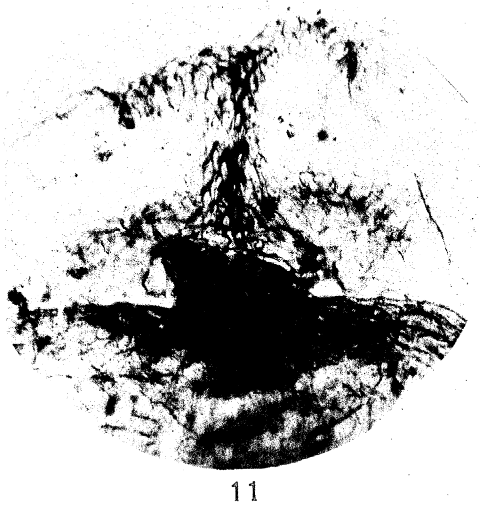

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H.H.T. photo.

Gristhorpia Nathorsti.

ZINCO COLLOTYPE CO. EDINBURGH.


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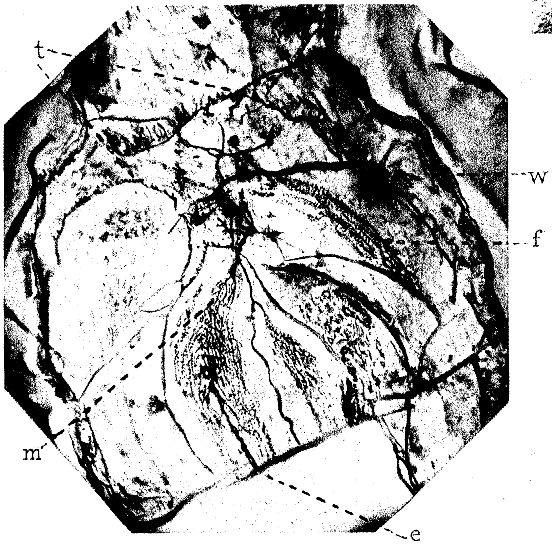

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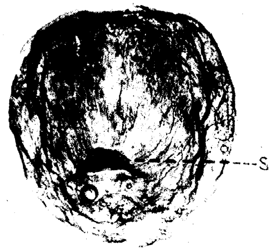

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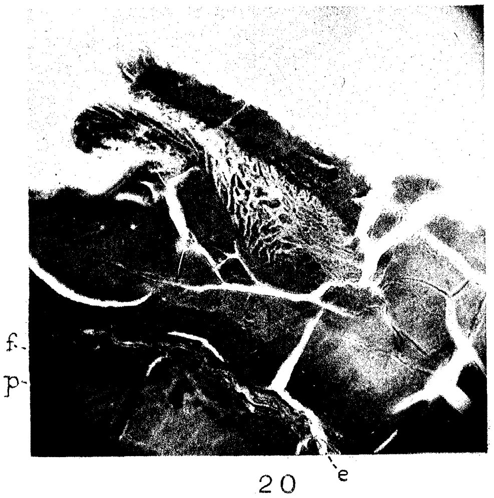

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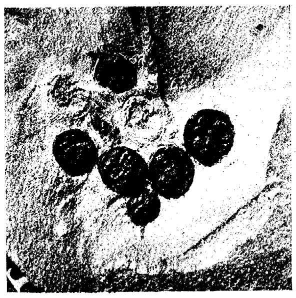
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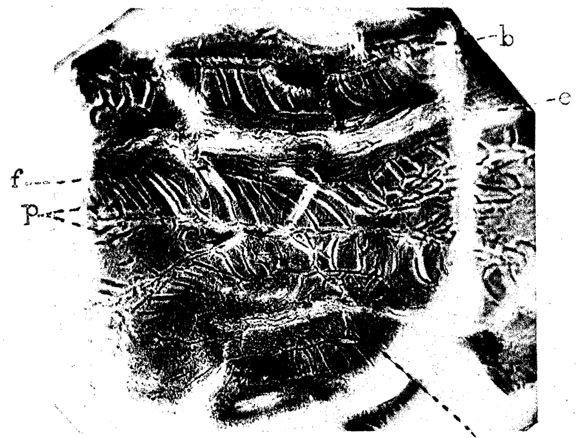
Caytonia Sewardi

Zinco Collotype Co., Edinburgh.



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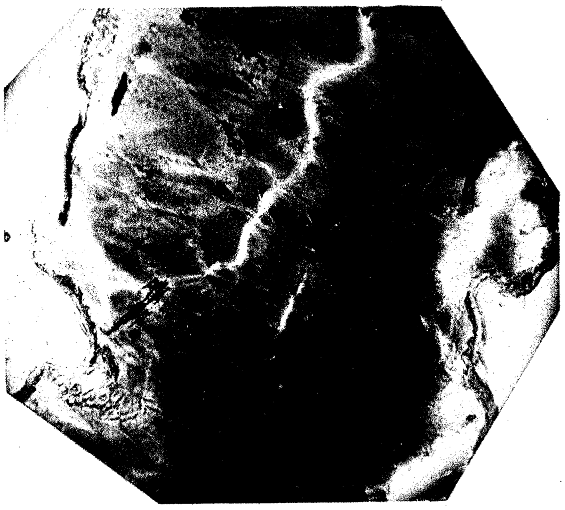

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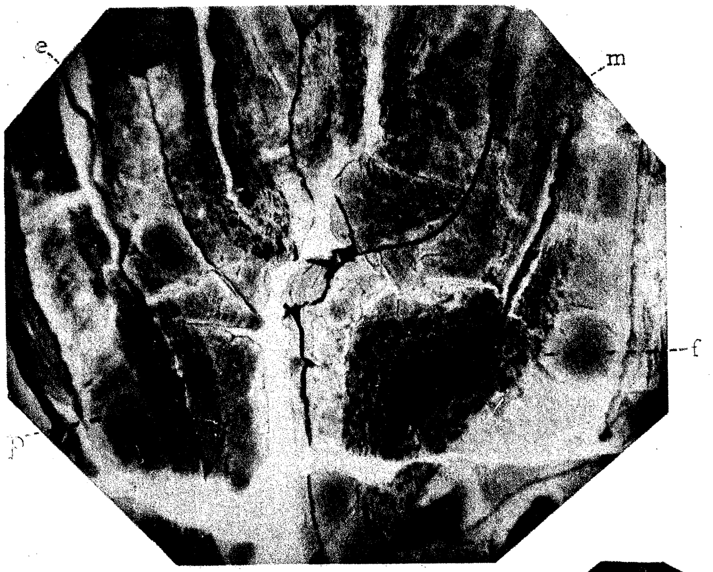

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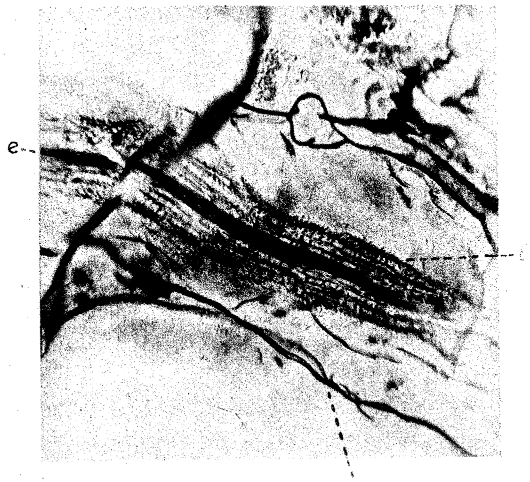

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H.H.T. photo.

Caytonia Sewardi

Zinco Collotype Co., Edinburgh.

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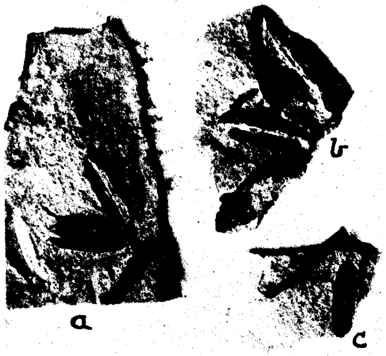

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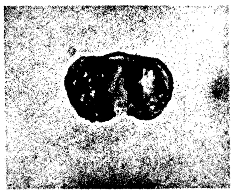

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H.H.T. photo.

Zinco Collotype Co. Edinburgh.

Antholithus Arberi and Gristhorpia Nathorsti.

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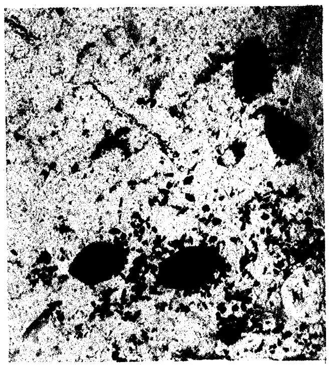

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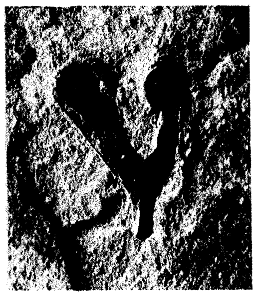

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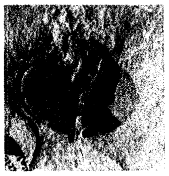

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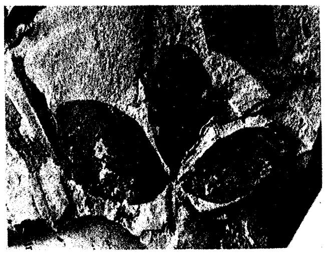

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Gristhorpia Nathorsti and Sagenopteris Phillipsi (Brongn)

ZINCO COLLOTYPE CO., EDINBURGH.

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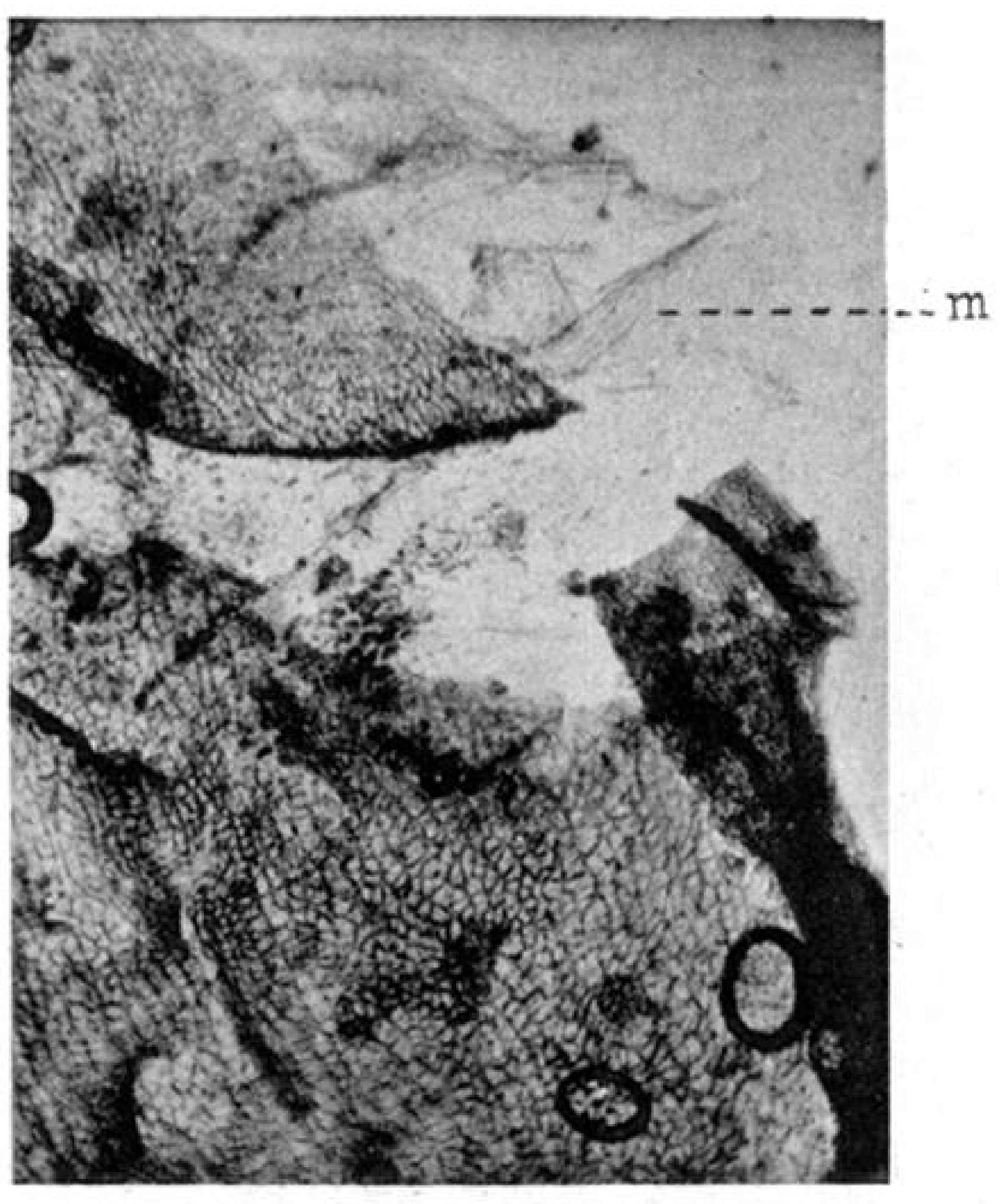

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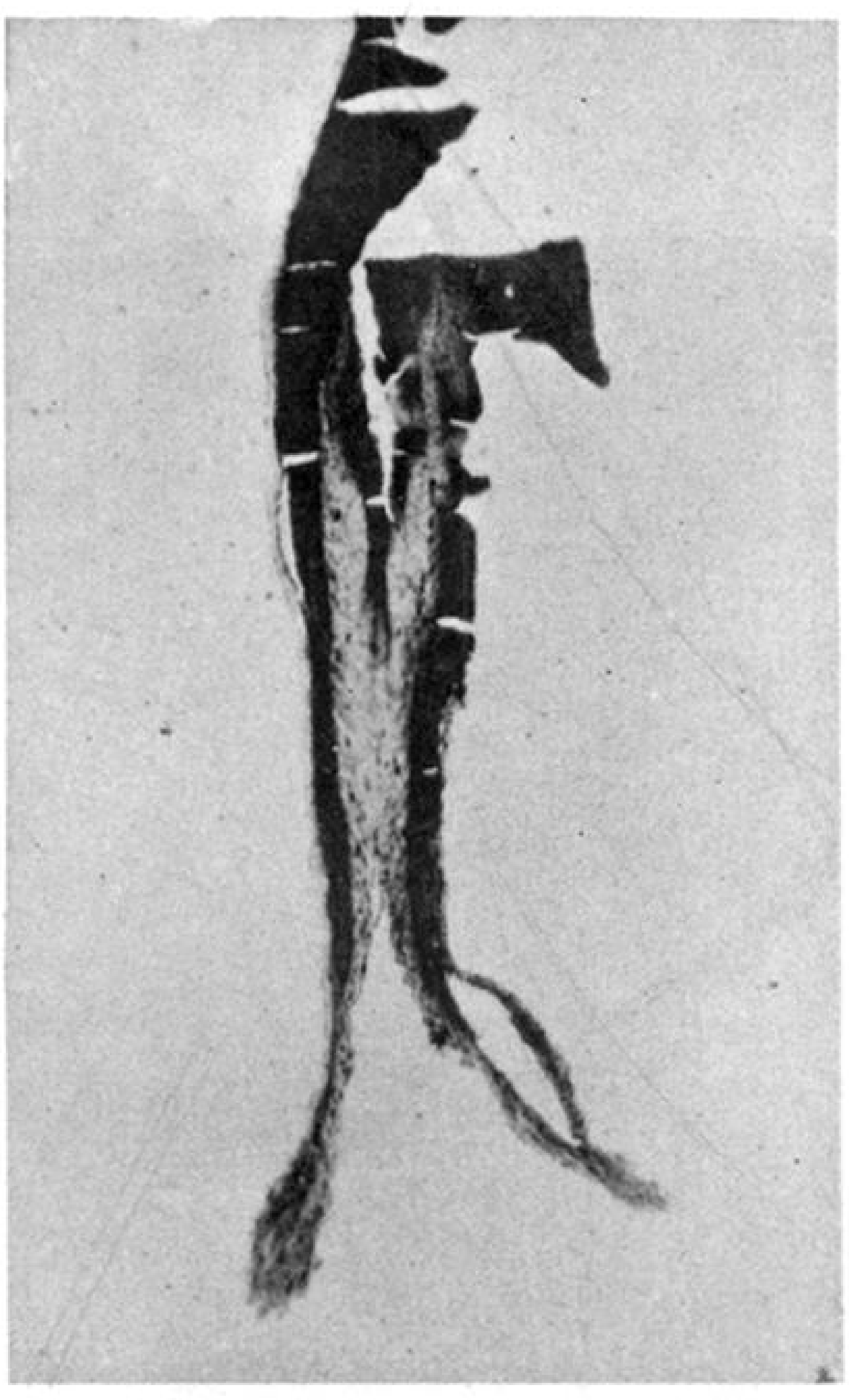

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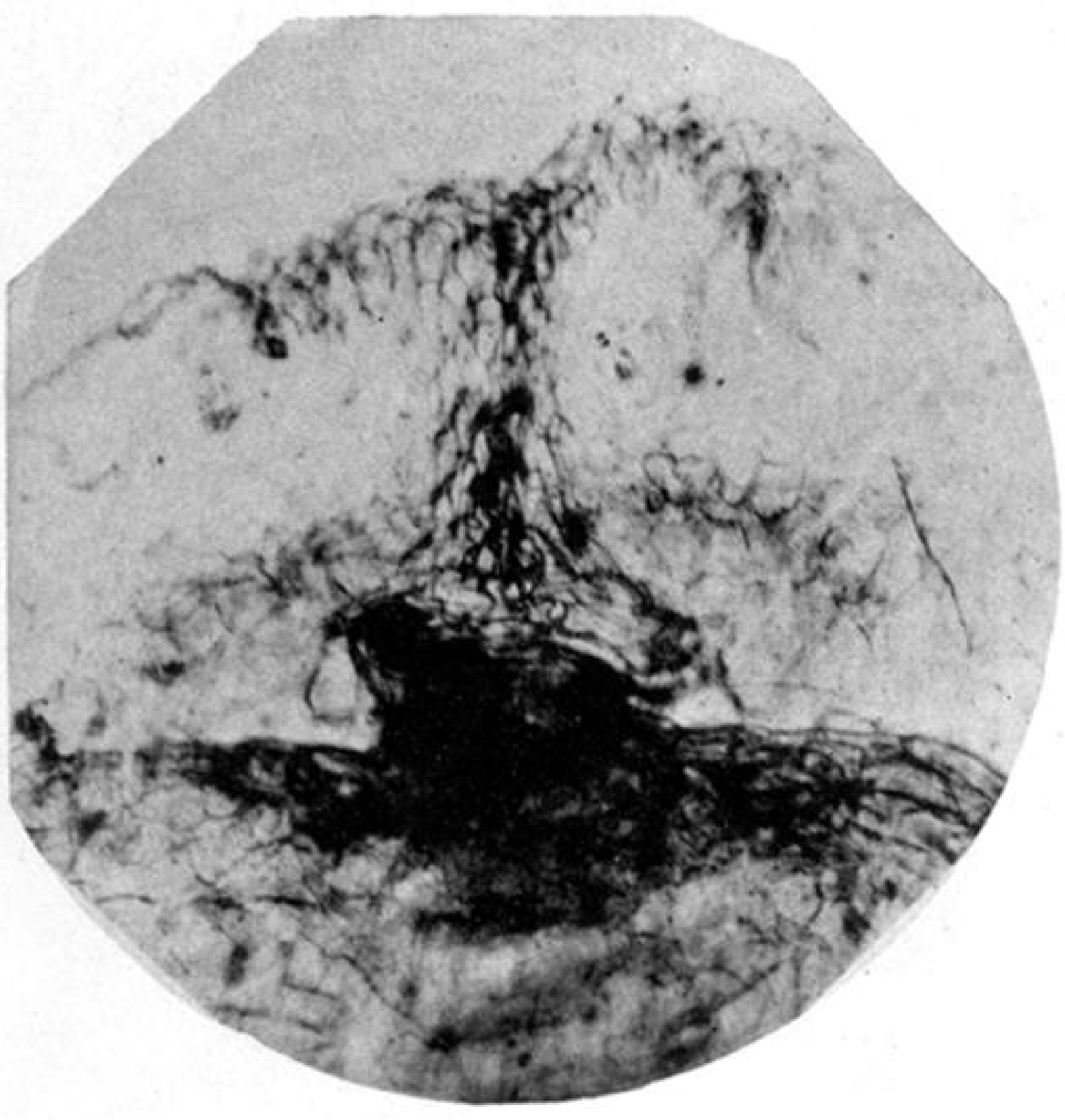

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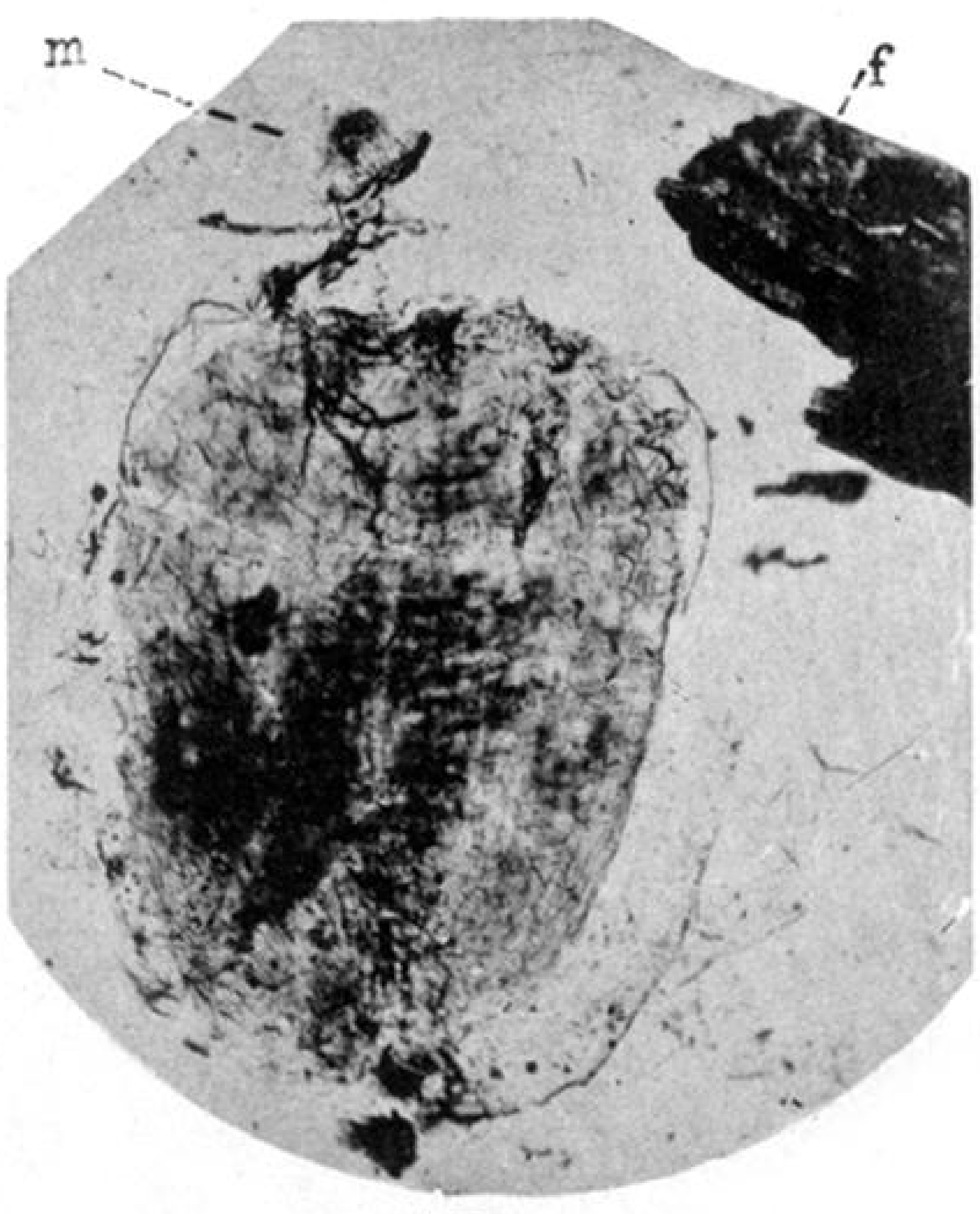

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PLATE 11.—*Gristhorpia Nathorsti* gen. et sp. nov.

Fig. 1.—Main axis showing a young fruit attached to it, and the scars (*s*) of two fruits which have become detached. A detached older fruit is seen above. × 2·5.

Fig. 2.—Part of a macerated fruit showing epidermis of the fruit wall and remains of membranes from the enclosed seeds (*m*). × 75.

Fig. 3.—Macerated specimen of an old fruit which has burst open at the top. The dark hump near the stalk on the left is the remains of the stigma. × 6.

Fig. 4.—One of the youngest specimens showing the main axis with a row of stalked carpels on one side. (The other row is buried in the matrix.) The preparation showing pollen grains on the stigma (Pl. 14, fig. 42) was obtained from one of these carpels. × 2·5.

Fig. 5.—Infructescence showing two rows of fruits. The central axis is buried in the matrix and is only exposed in one place in the centre. Nat. size.

Fig. 6.—Two young fruits showing their pedicels and the stigmatic flaps near their bases. × 2·5.

Fig. 7.—Young fruit detached from the matrix showing longitudinal wrinkling, stigma and pedicel. × 5.

Fig. 8.—Old fruit burst open with isolated seed lying near. × 2.

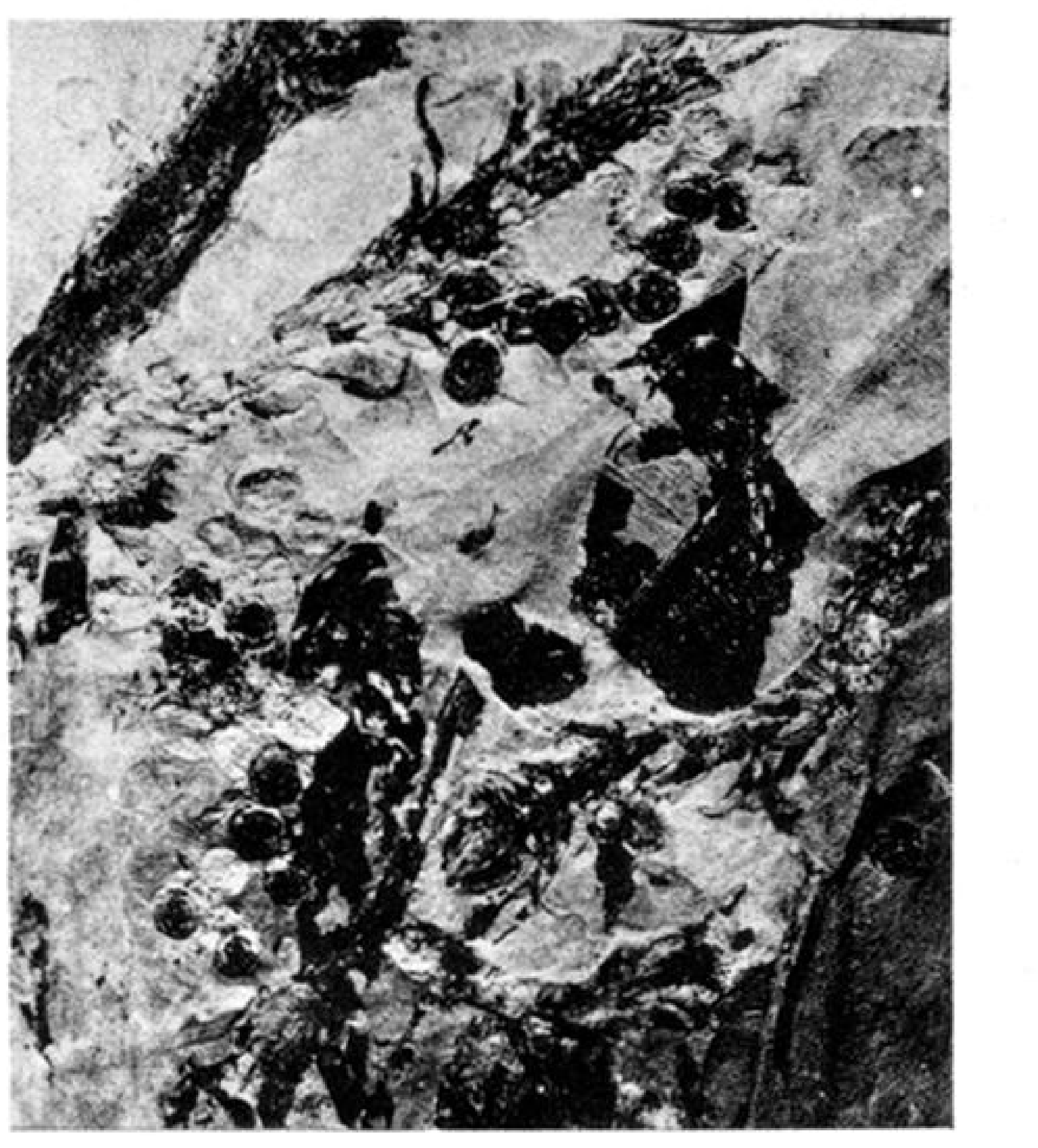
Fig. 9.—Old fruit showing apical fissure. × 2.

Fig. 10.—Longitudinal section of stigma of specimen shown in text-fig. 3, showing the inverted funnel shaped opening lined with lighter, cutinised cells which extend upwards into the centre of the fruit, thinning out again into two points. The substance of the fruit is irregularly fractured above. × 54.

Fig. 11.—Apical part of macerated seed shown in fig. 12. Note dark megaspore membrane with plinth-like flange at the top; above this are the cutinised cells lining the micropyle. The external cells of the inner integument are papillate. *Cf.* text-fig. 4. × 185.

Fig. 12.—Complete macerated seed, showing in the centre the megaspore membrane, with the micropyle at its apex. The thin line surrounding the seed is the remains of the inner wall of the blow-off layer, and the space below it shows the position of the palisade layer. Some cells of the parenchymatous layer, which possibly corresponds to the inner integument, are seen near the micropyle. × 28.

Fig. 13.—Remains of the seed membranes extracted from a closed fruit. They were somewhat broken up in extraction, but the characteristic cells lining the micropyle are seen at *m*. Remains of the fruit wall are seen at *f*. × 32.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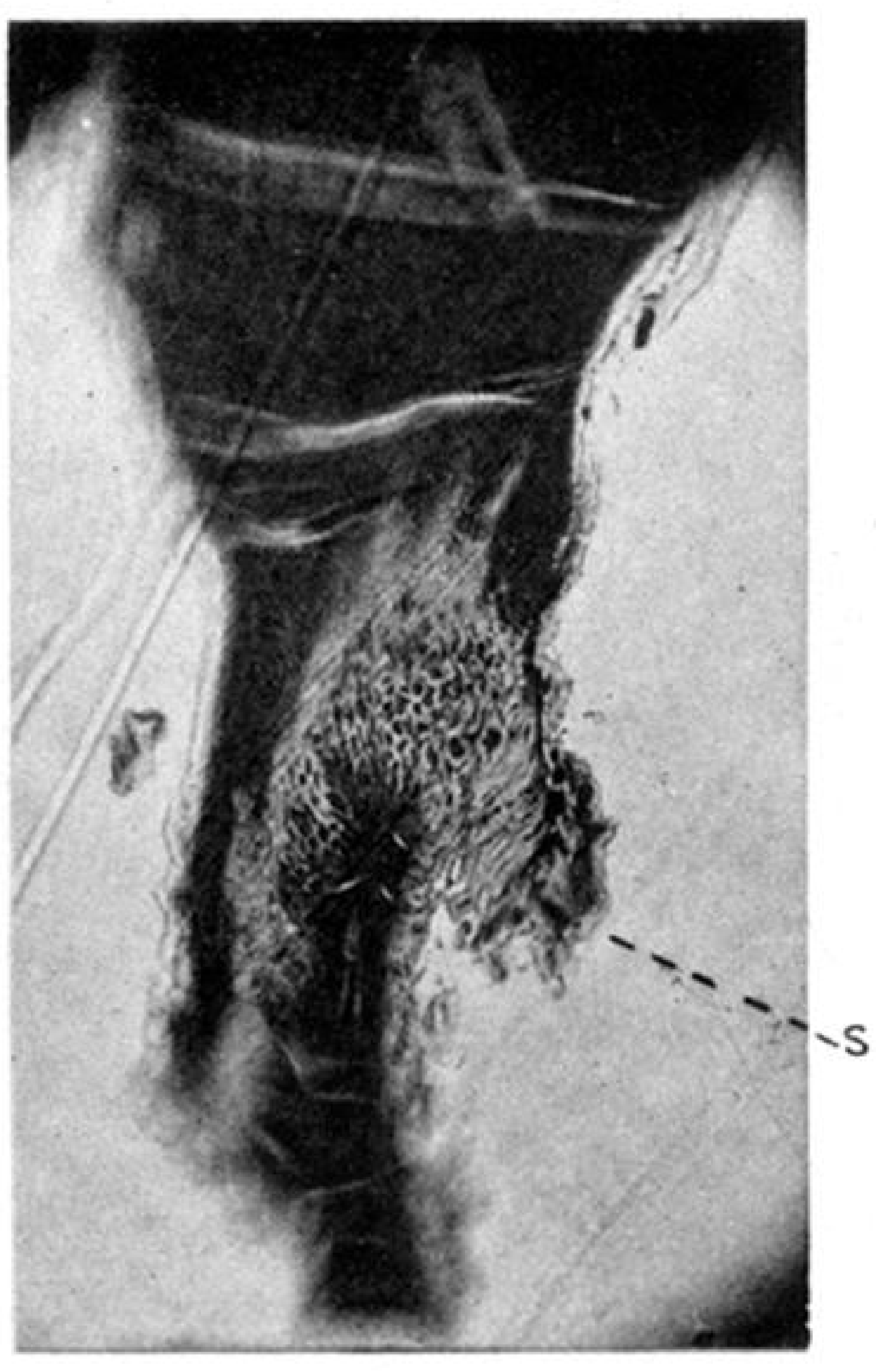

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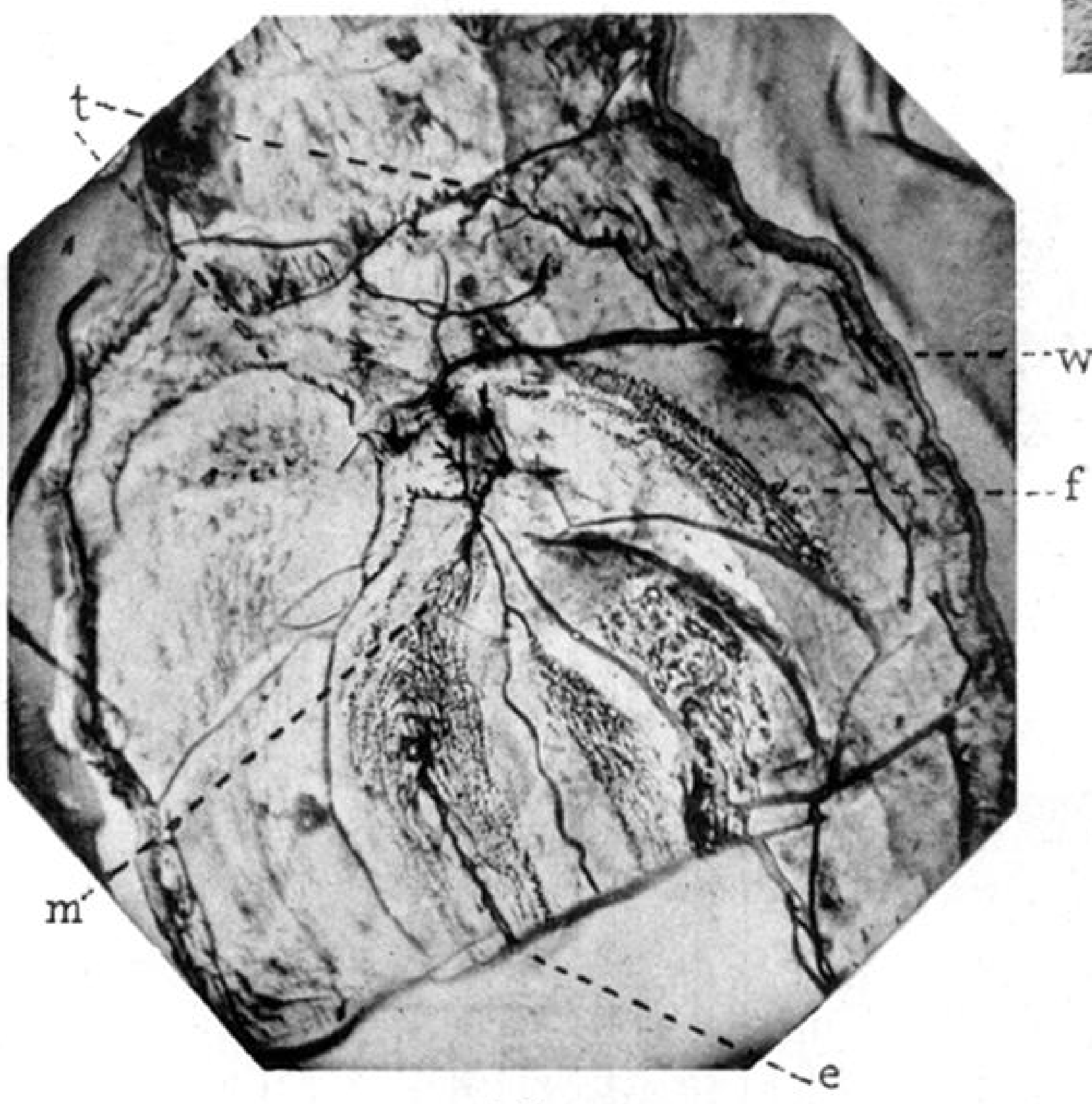

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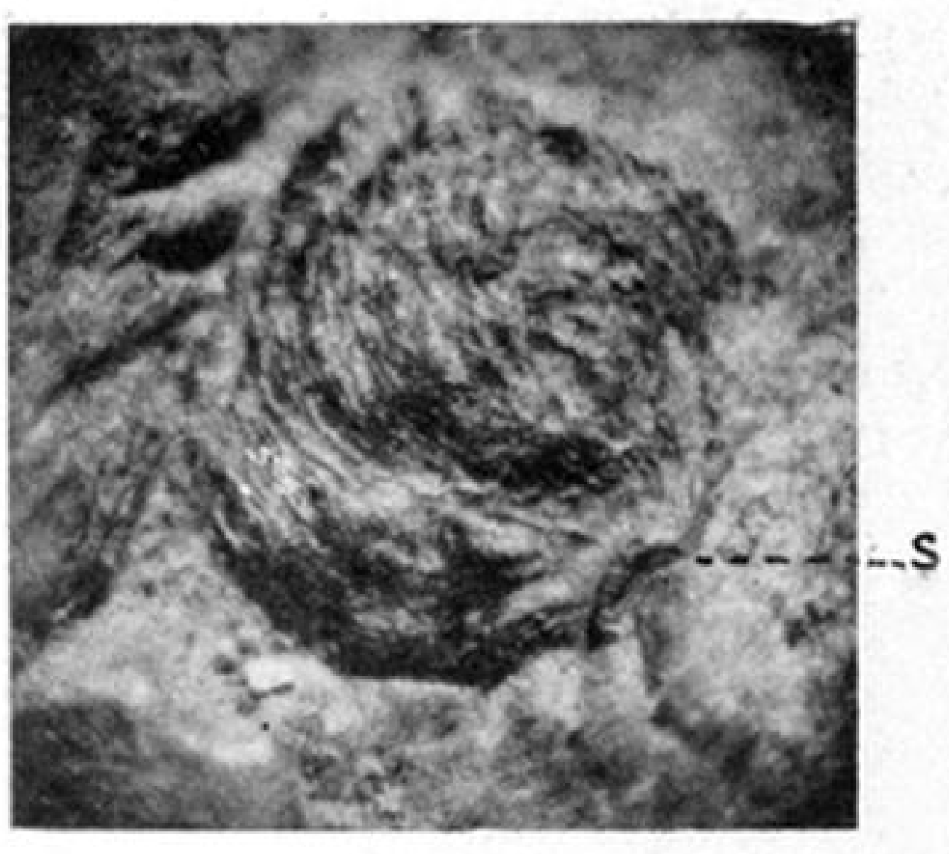

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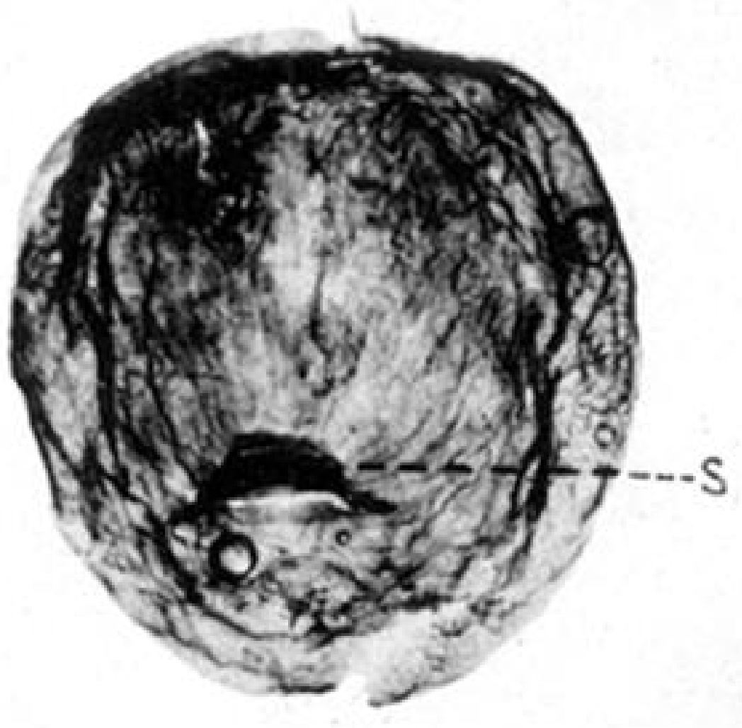

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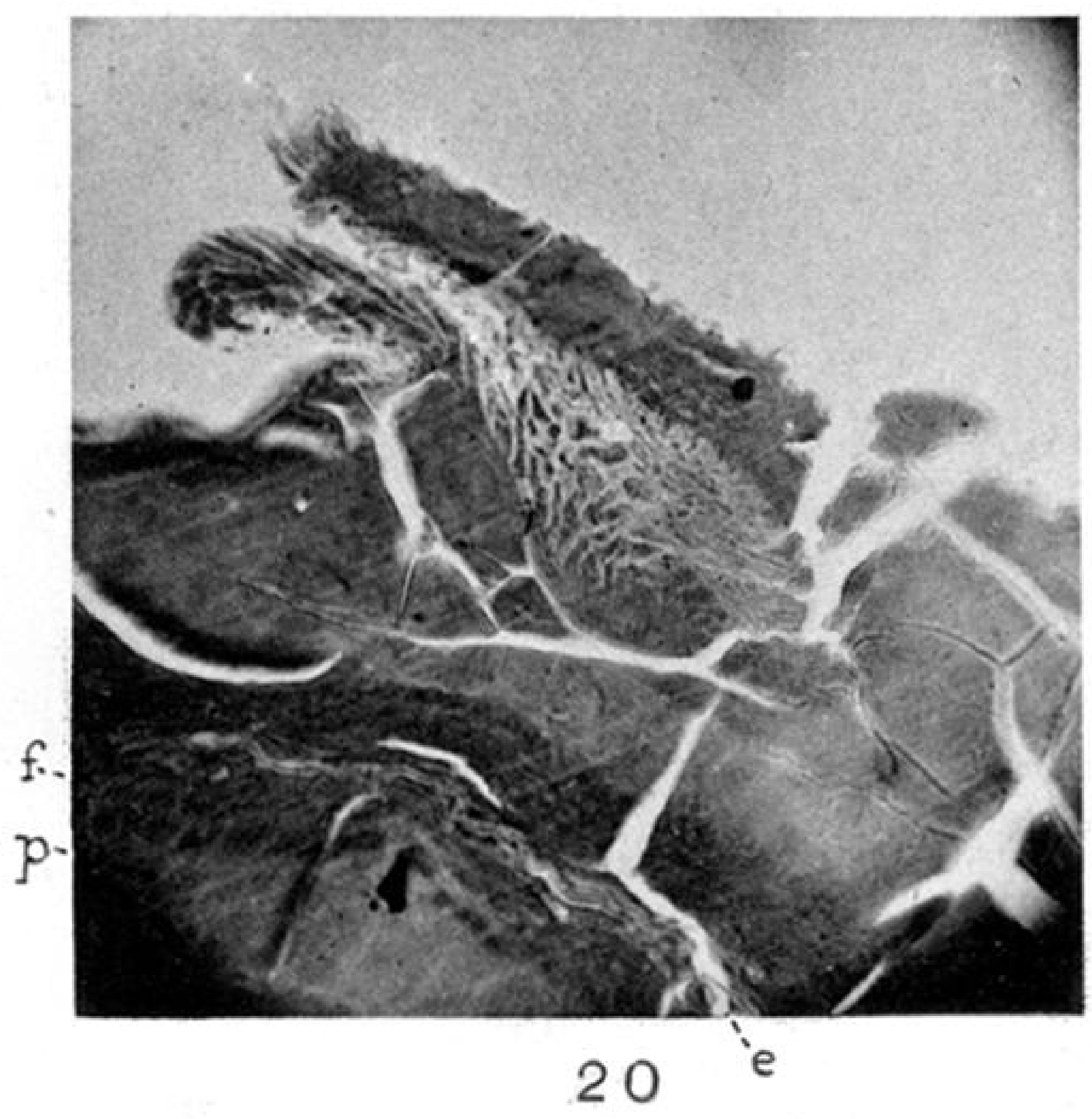

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PLATE 12.—*Caytonia Sewardi* gen. et sp. nov.

Fig. 14.—Specimen showing the remains of two infructescences, with leaves of *Sagenopteris*, *Pagiophyllum* and *Taeniopteris*. Nat. size.

Fig. 15.—Magnified view of the upper infructescence shown in fig. 14. The fruits are lying on top of the axis, which is only seen near the base. × 2·5.

Fig. 16.—Part of an infructescence showing its attachment to a larger branch, also isolated fruits in which the outlines of seeds can be made out. No perianth scars can be found on the axis or on the branch. × 2·5.

Fig. 17.—Single fruit embedded in the matrix showing flange-like stigma (*s*) at the base. The pedicel is only just visible. × 9.

Fig. 18.—Longitudinal section of a fruit passing through the stigma somewhat tangentially. The pedicel is seen below and the stigmatic flange at *s*. Note the cutinised cells lining the stigma and spreading inwards. *Cf.* with fig. 20. This section was not chemically treated after cutting and no structure is seen in the upper part. × 109.

Fig. 19.—Section of a fruit (series Z) cleared with Schultz's fluid and dilute ammonia. Part of the structure of four seeds is shown. The thick cuticle of the fruit wall is seen at *w*; the remains of a fibrous layer at *f* and in other places; the teeth on the outside of the seeds left by the solution of the blow-off layer at *t*. The section at *m* passes through a micropyle. A megaspore membrane is seen at *e*. × 106.

Fig. 20.—Median longitudinal section through a stigma compressed on the side of an isolated fruit. The stigmatic opening lined with cutinised cells is seen, with part of the pedicel above and the stigmatic flap below. Note the extension of the cutinised cells into the fruit. Just below a seed is seen in which the structure is visible. The megaspore membrane *e* is surrounded by darker cells, the fibres *f*, outside which is the palisade layer *p*. The seed is close up against the fruit wall at the point where the stalk enters, which seems to exclude the possibility of the occurrence of an axile placenta. Section cleared with hydrochloric acid and potassium chlorate followed by sodium sulphite. × 109.

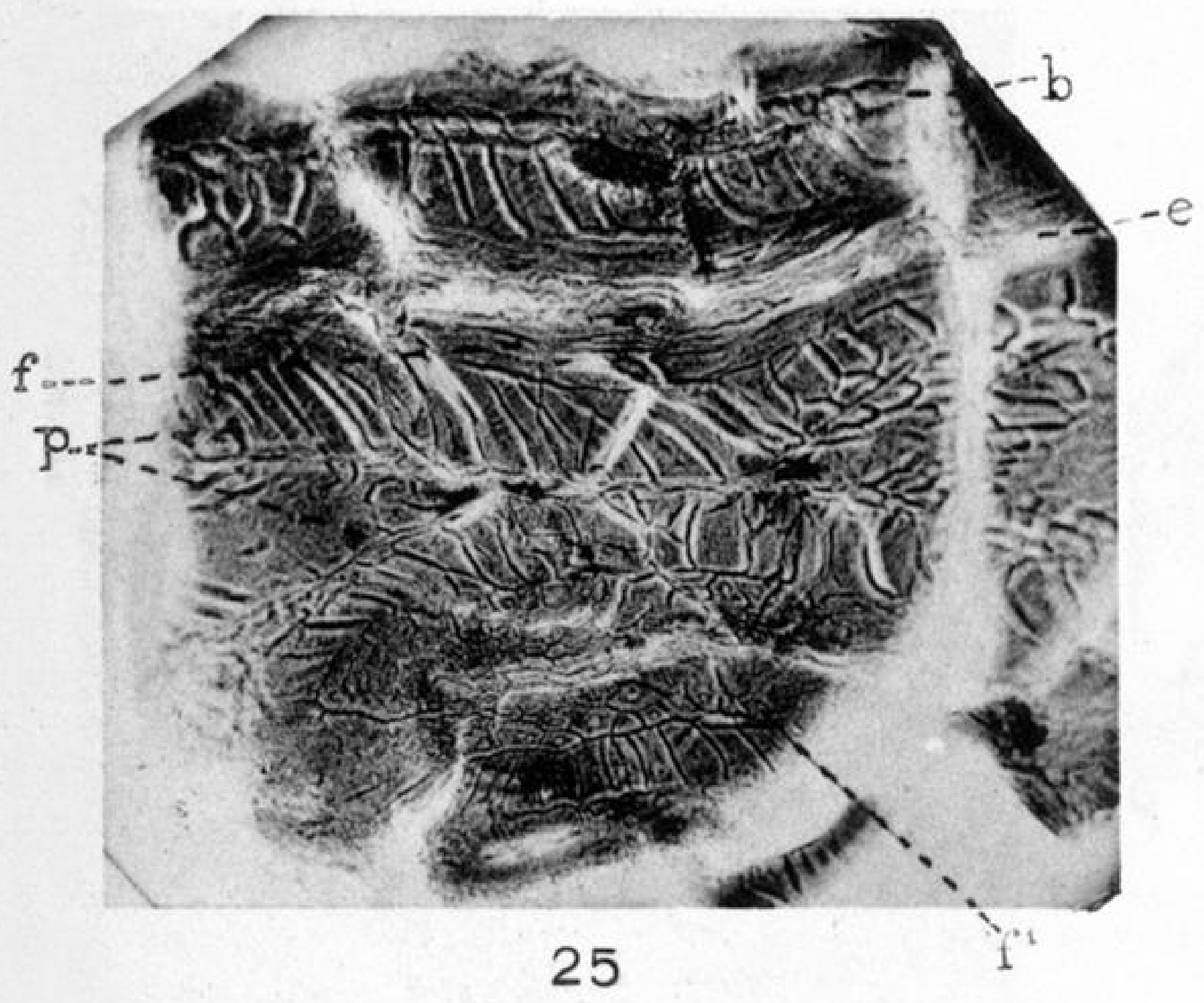
Fig. 21.—Isolated seeds in a hand specimen in which they occur in large numbers. × 4.

Fig. 22.—Group of separate fruits showing clearly the enclosed seeds. Nat. size.

Fig. 23.—Macerated fruit. Only the cuticle of the fruit wall remains with the remains of seeds (not shown) inside. The dark piece at *s* is the remains of the stigma; the pedicel was detached from the point below the stigma, where a small gap is seen. × 5.

Fig. 23A.—Isolated fruit detached from the matrix, similar to the examples which were cut into sections. The stigma occurs at *s*, but is not clearly shown. × 3.

Fig. 24.—Isolated detached fruit from which the wall had been broken away showing seeds inside. × 3.



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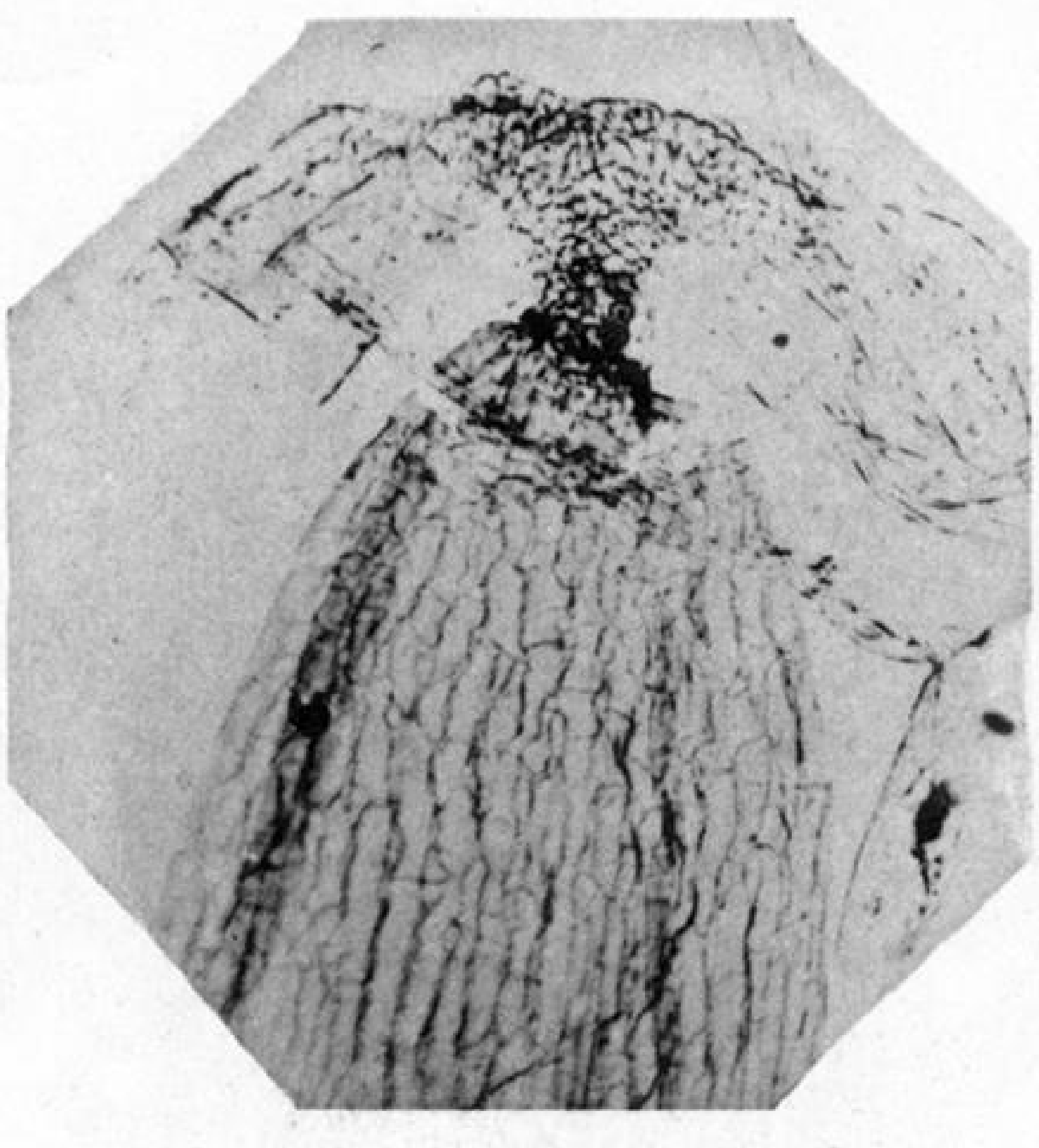

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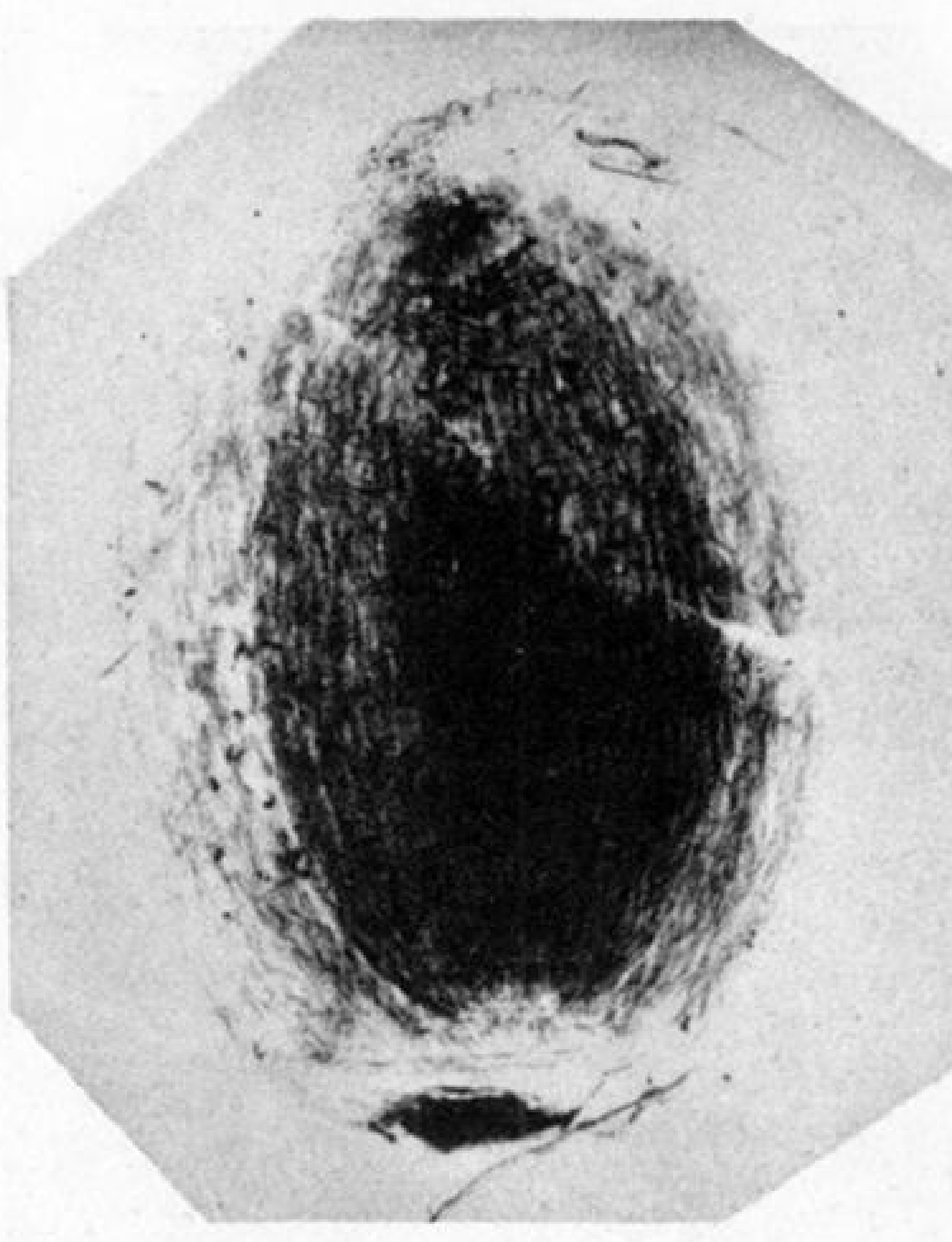

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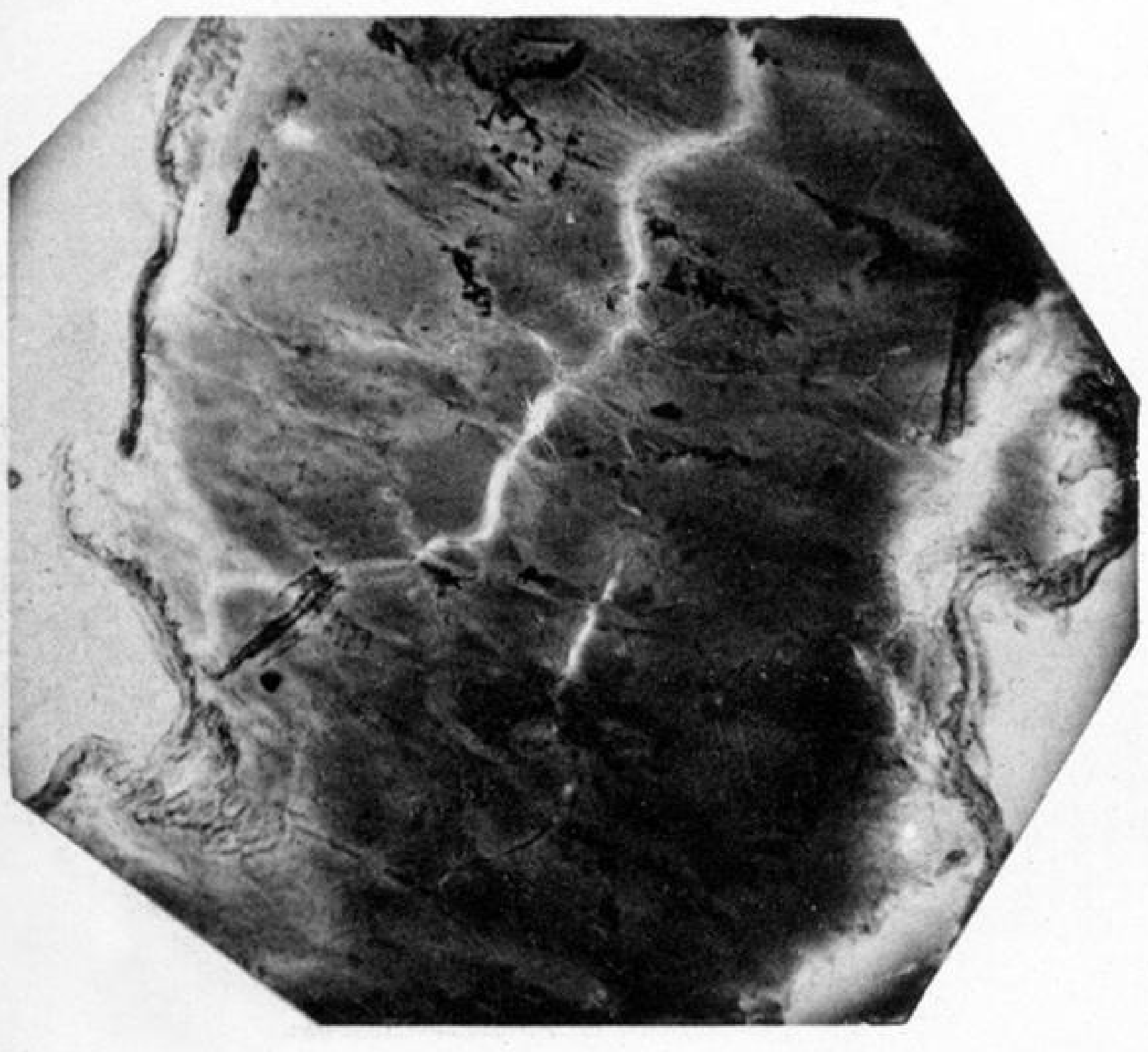

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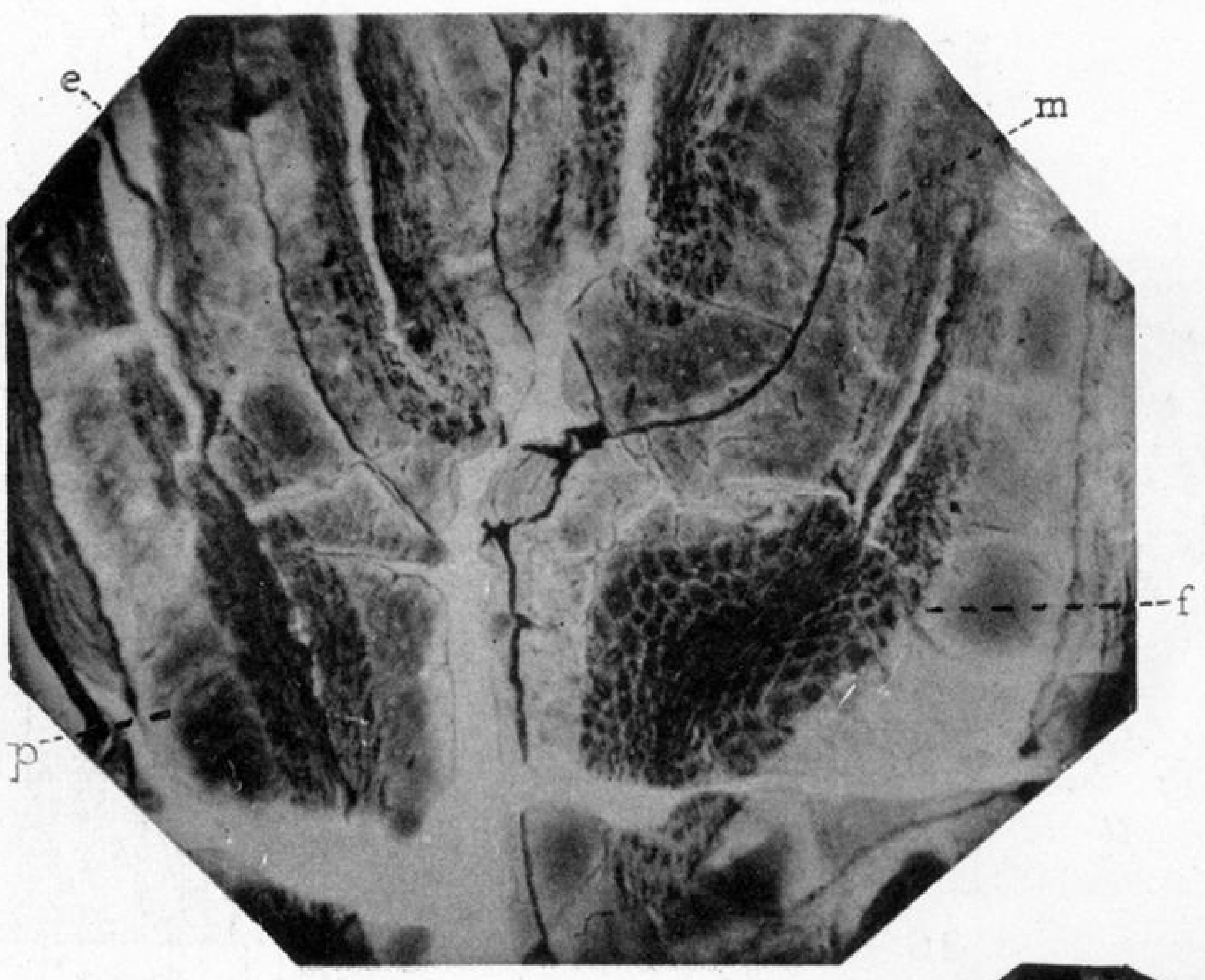

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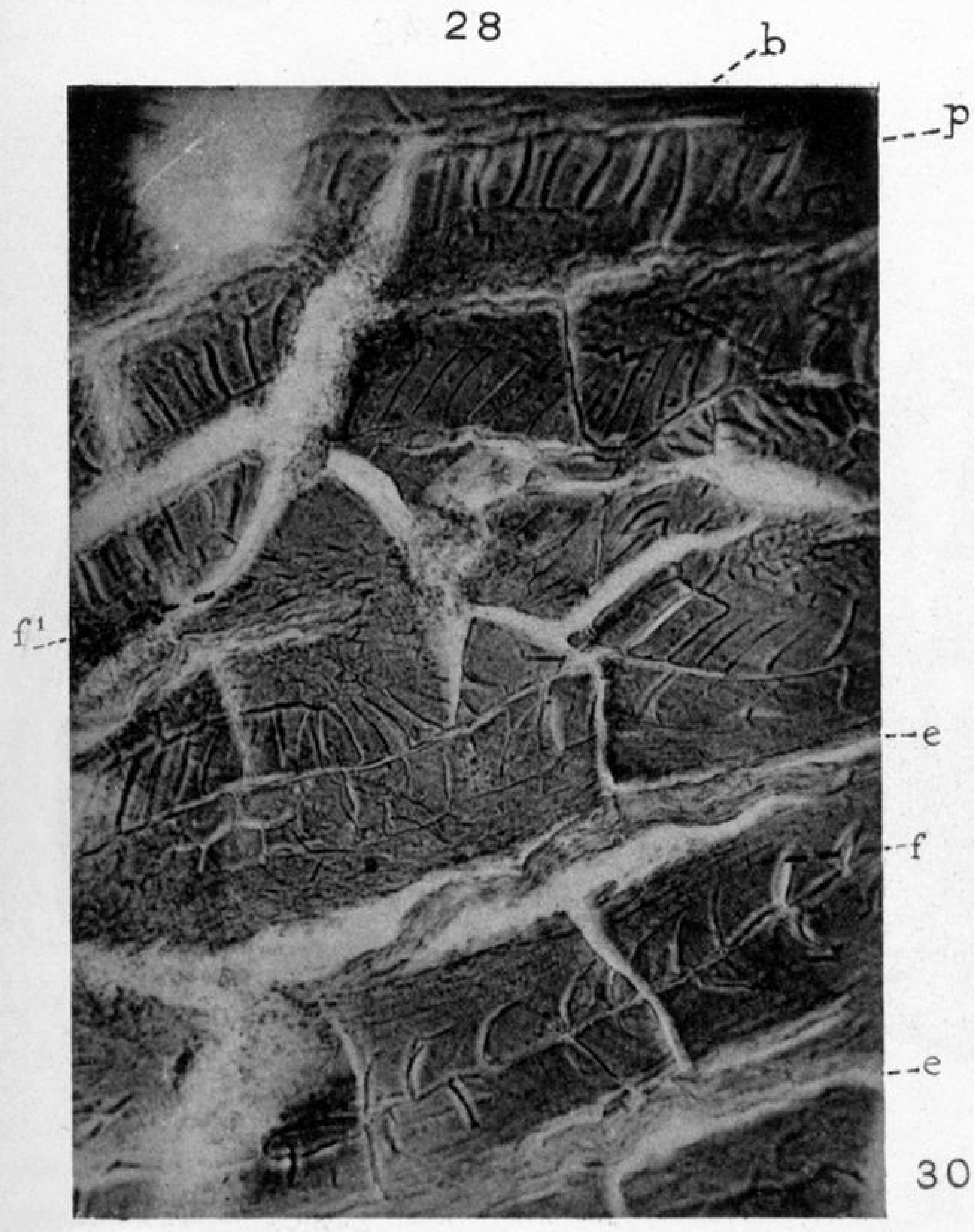

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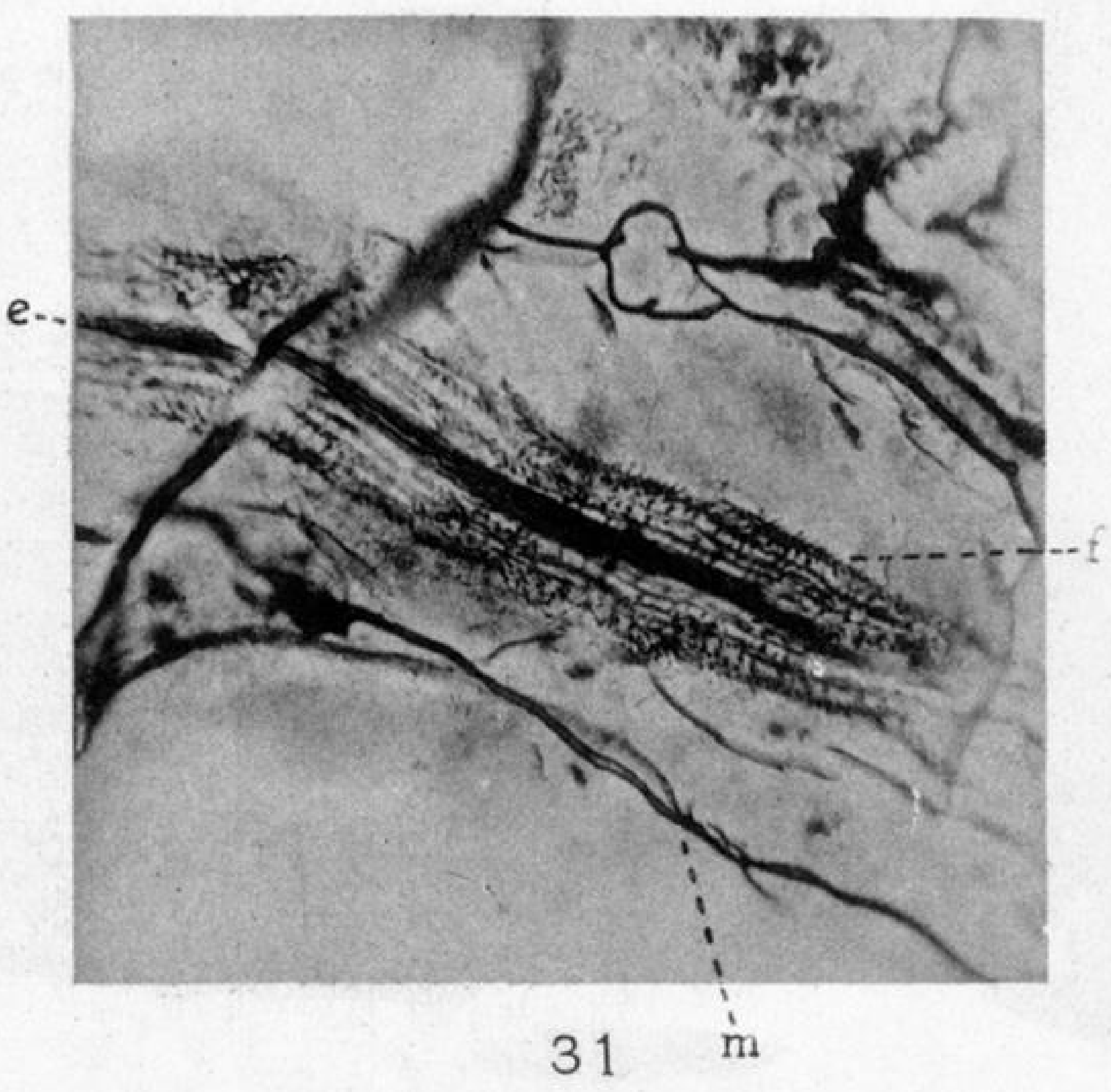

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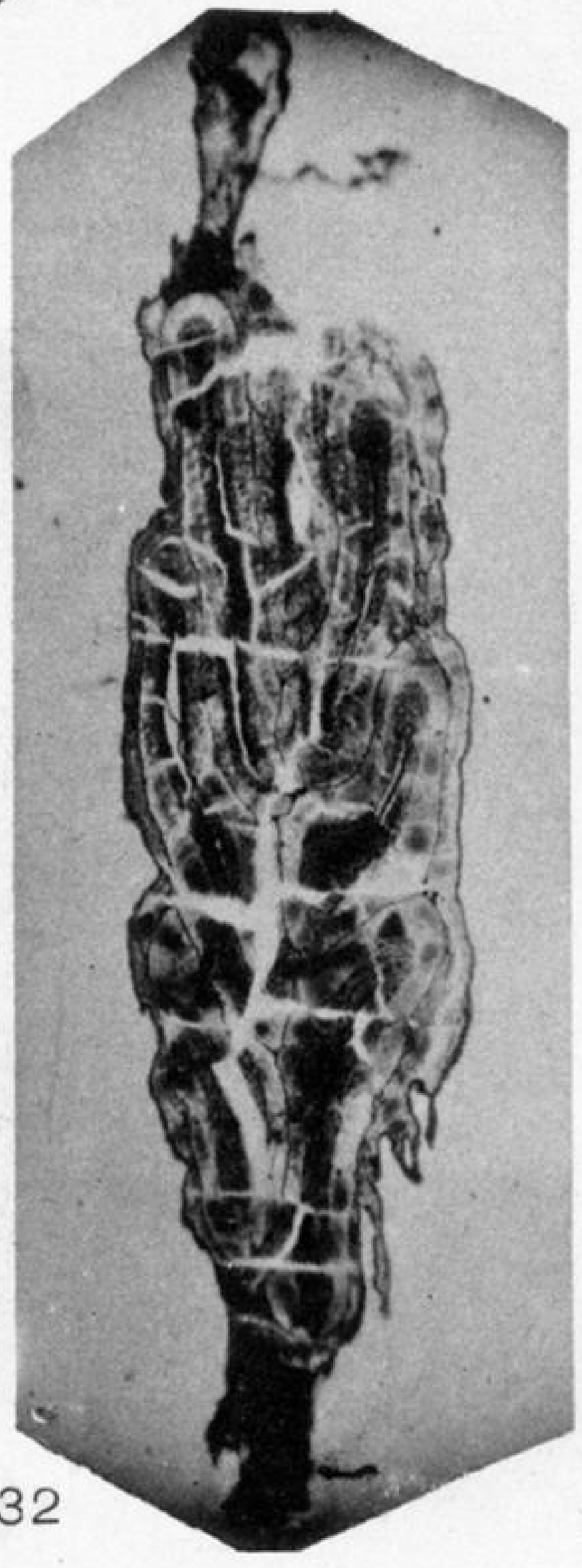

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Plate 13.—*Caytonia Sewardi* gen. et sp. nov.

Fig. 25.—Section through a fruit after treatment with Schultz's fluid followed by alcohol and formalin. The middle lamellæ of the cells are now visible. In the upper part a seed is seen in longitudinal section. In the lower part another seed has been cut more transversely. *b*. Blow-off layer which is only seen near the fruit wall. *e*. Megaspore membranes (and remains of embryo ?) *p*. Palisade layer. *f*. Fibres in longitudinal section. *f'*. Fibres in transverse section. × 108.

Fig. 26.—Apical part of an isolated seed after prolonged maceration and clearing, showing the megaspore membrane and the cutinised cells of the micropyle. The outer cuticle of the seed is just visible round the flange of micropylar cells at the apex. *Cf.* text-fig. 9. × 75.

Fig. 27.—Isolated seed which has been macerated and partly cleared, showing the remains of the fibres round the megaspore membrane. A dark spot marks the point of attachment, but the micropyle at the upper end is not clearly seen. × 32.

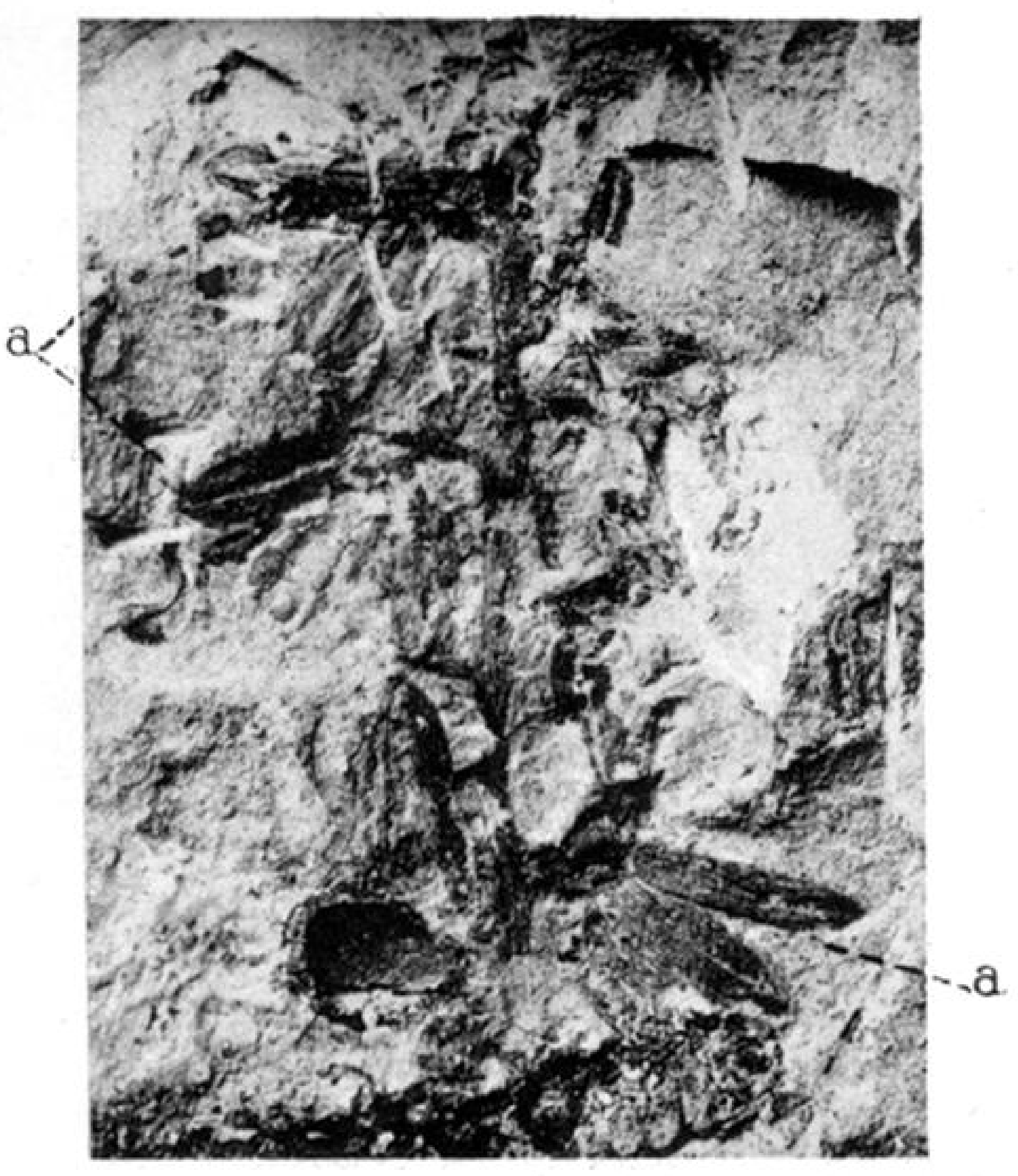
Fig. 28.—Tangential section through the wall of the fruit (after treatment by sodium sulphite method). Note the thick cuticle and the remains of large irregular cells which may have been fleshy during life. × 200.

Fig. 29.—Part of the longitudinal section through the fruit shown in fig. 32 (series Z, after treatment by alcoholic ammonia method). Parts of four seeds are seen. The seeds are separated by a cutinised membrane *m*, no trace of a blow-off layer remaining. The fibrous layers *f* are clearly seen and the palisade layer *p* is faintly visible. In the centre of each seed the megaspore membrane *e* appears, with little or no trace of a contained embryo. × 126.

Fig. 30.—Section of a fruit (series O) treated in the same way as that shown in fig. 25. Parts of five seeds are seen. The blow-off layer is only seen in one place. Lettered as in fig. 25. × 108.

Fig. 31.—Part of a section through a seed after somewhat prolonged clearing with alcoholic ammonia, showing the remains of the outer cuticle of the seed coats (*m*) and spicule-like remains of fibres *f* on both sides of the megaspore membrane *e*. × 220.

Fig. 32.—Complete longitudinal section of a fruit showing seven seeds within. The stigma was at the bottom of the section, and the club-shaped projection at the top was formed from the fruit wall. The seeds occupy similar positions to those shown in text-fig. 8. The central portion, more highly magnified, is shown in fig. 29. × 30.



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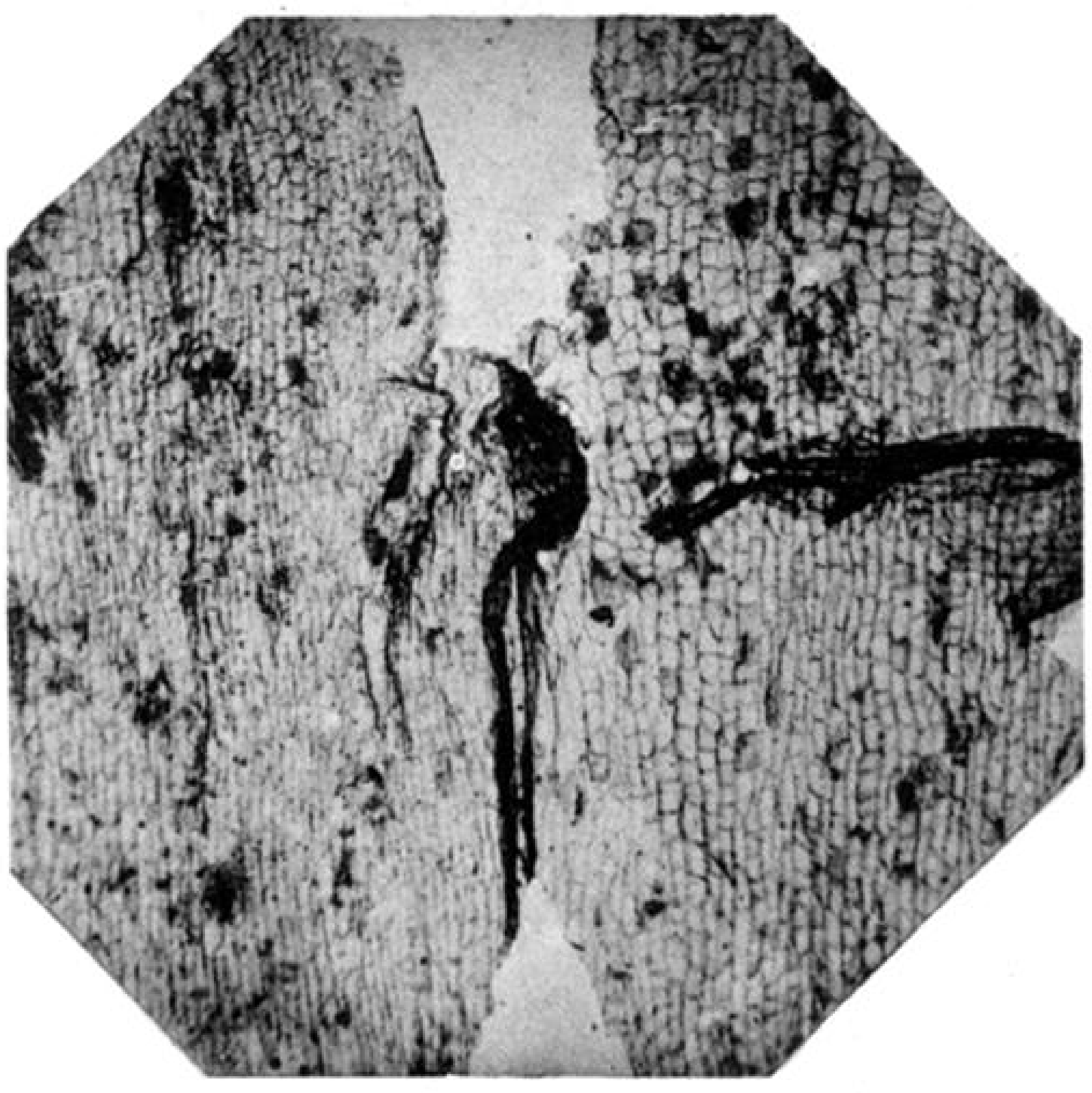

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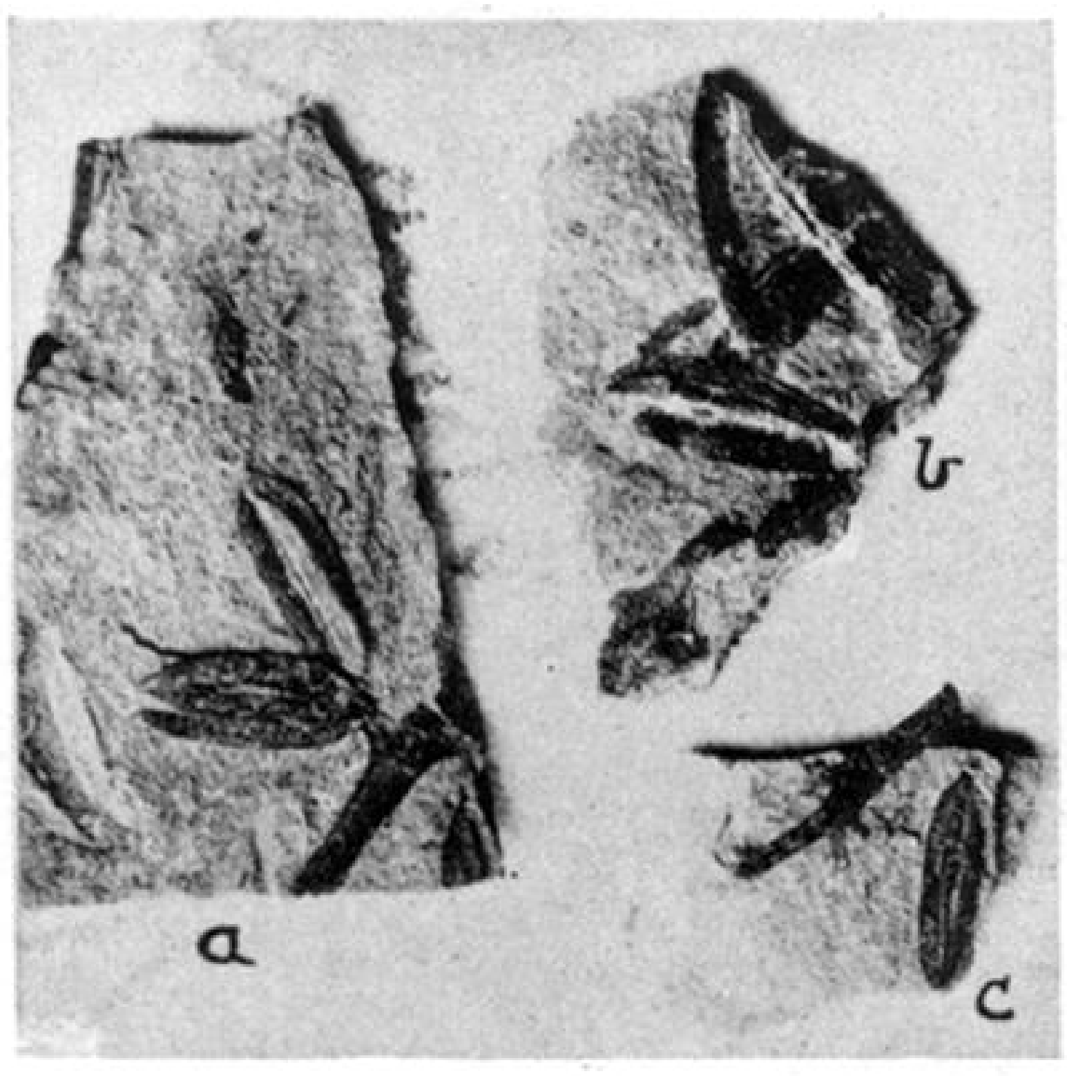

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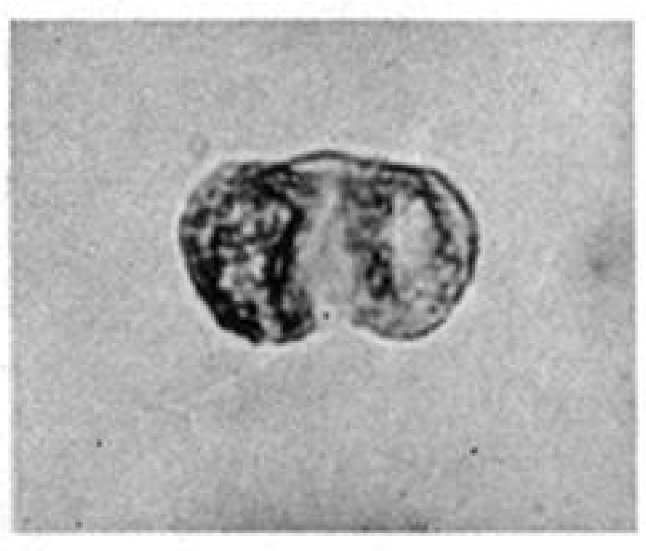

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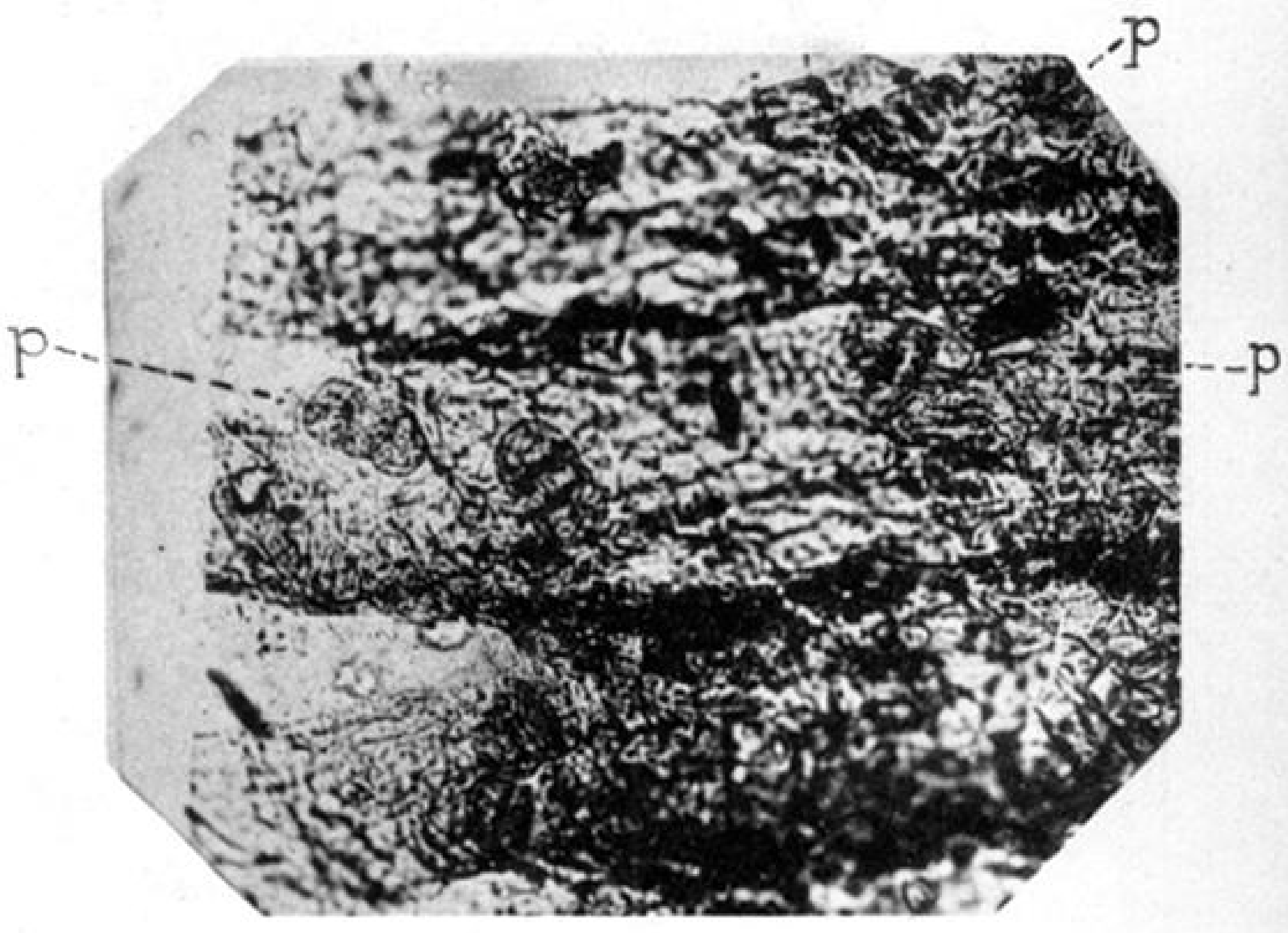

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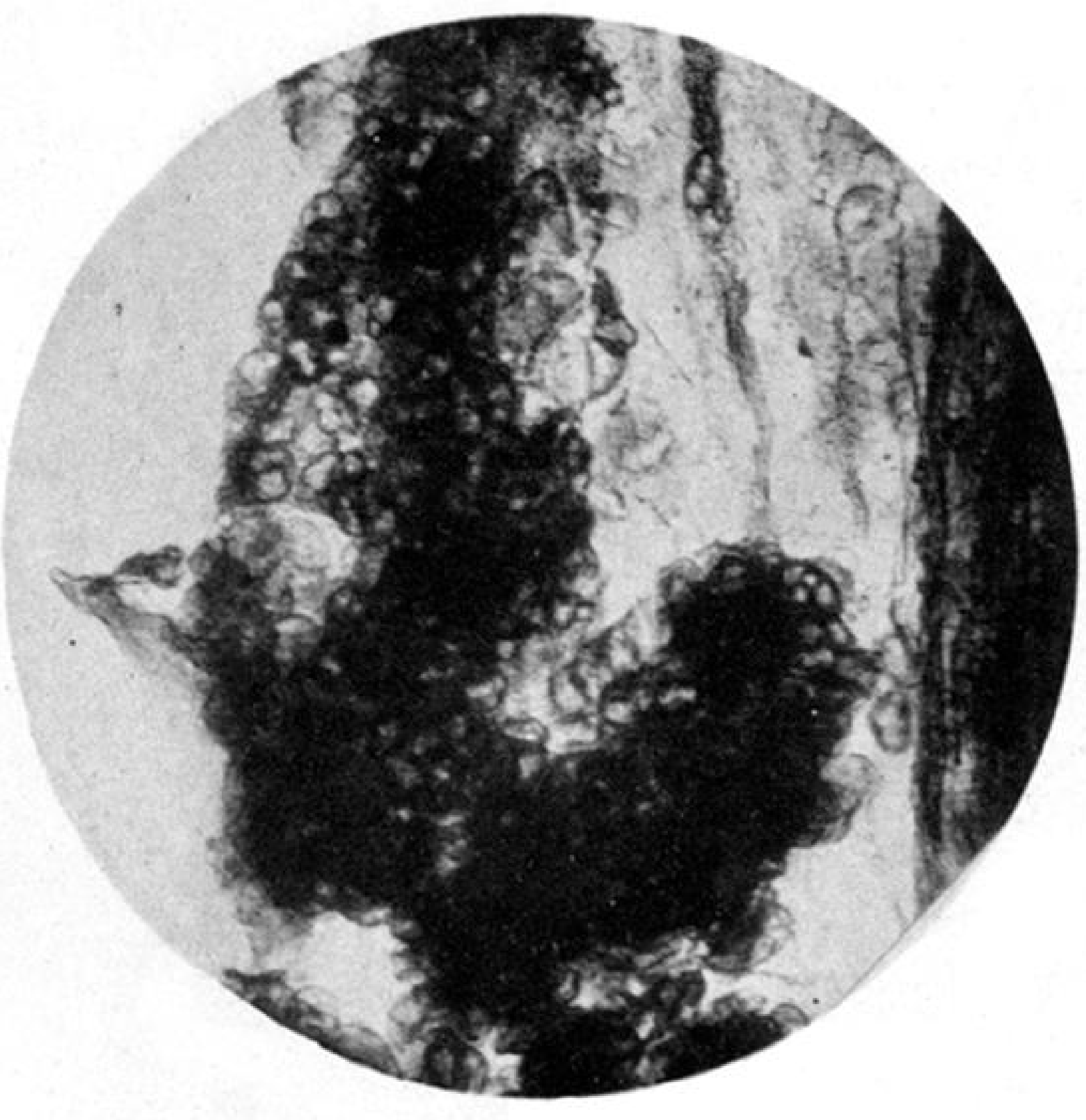

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Antholithus Arberi and Gristhorpia Nathorsti.

PLATE 14.—*Antholithus Arberi* sp. nov.

Fig. 33.—Largest specimen showing the central axis and side branches to some of which anthers, *a*, are still attached. × 3.

Fig. 34.—Cuticle preparation from the main axis showing the difference in the size and shape of the cells on the two sides. The right-hand portion of the preparation comes from one side, the left-hand portion from the opposite face. × 50.

Fig. 35.—Specimen showing the scattered remains of anthers and the stalks on which they were borne. × 3.

Fig. 36.—*a*. Part of a main axis with short side branch and two anthers, showing their four-lobed form. *b*. Fragments of anthers in which the lobes have become separated. *c*. Single anther and branch bearing forked appendages on which the anthers were borne. × 3.

Fig. 37.—Part of main axis bearing side branches (pinnæ) detached from the rock; the forking of one of the side branches is shown. × 5.

Fig. 38.—A single pollen grain, extracted from the interior of an anther, showing the two lateral wings with granular surface markings. × 600.

Fig. 39.—Tip of an anther which has been macerated, showing three of the four lobes still united at their tips; the elongated epidermal cells can just be made out. × 30.

Fig. 40.—Mass of winged pollen grains extracted from a macerated anther. × 220.

Gristhorpia Nathorsti gen. et sp. nov.

Fig. 41.—Cuticle preparation from part of the main axis of a young infructescence (sporophyll), showing the difference in the thickening and size of the epidermal cells on the two sides. The lateral margin of the axis is represented by the dark mass in the centre of the preparation. *Cf.* text-fig. 11, A.B. × 40.

Fig. 42.—Cuticle preparation of part of the stigma of a carpel or young fruit which shows at *p* a number of winged pollen grains identical with that shown in fig. 38. × 230.


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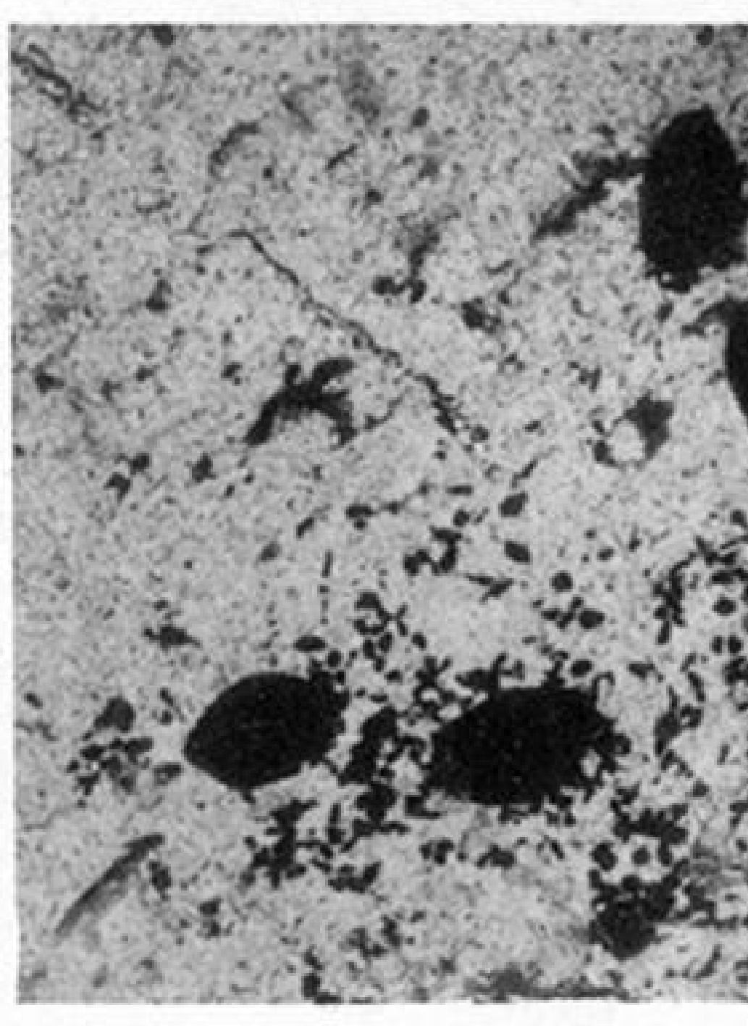
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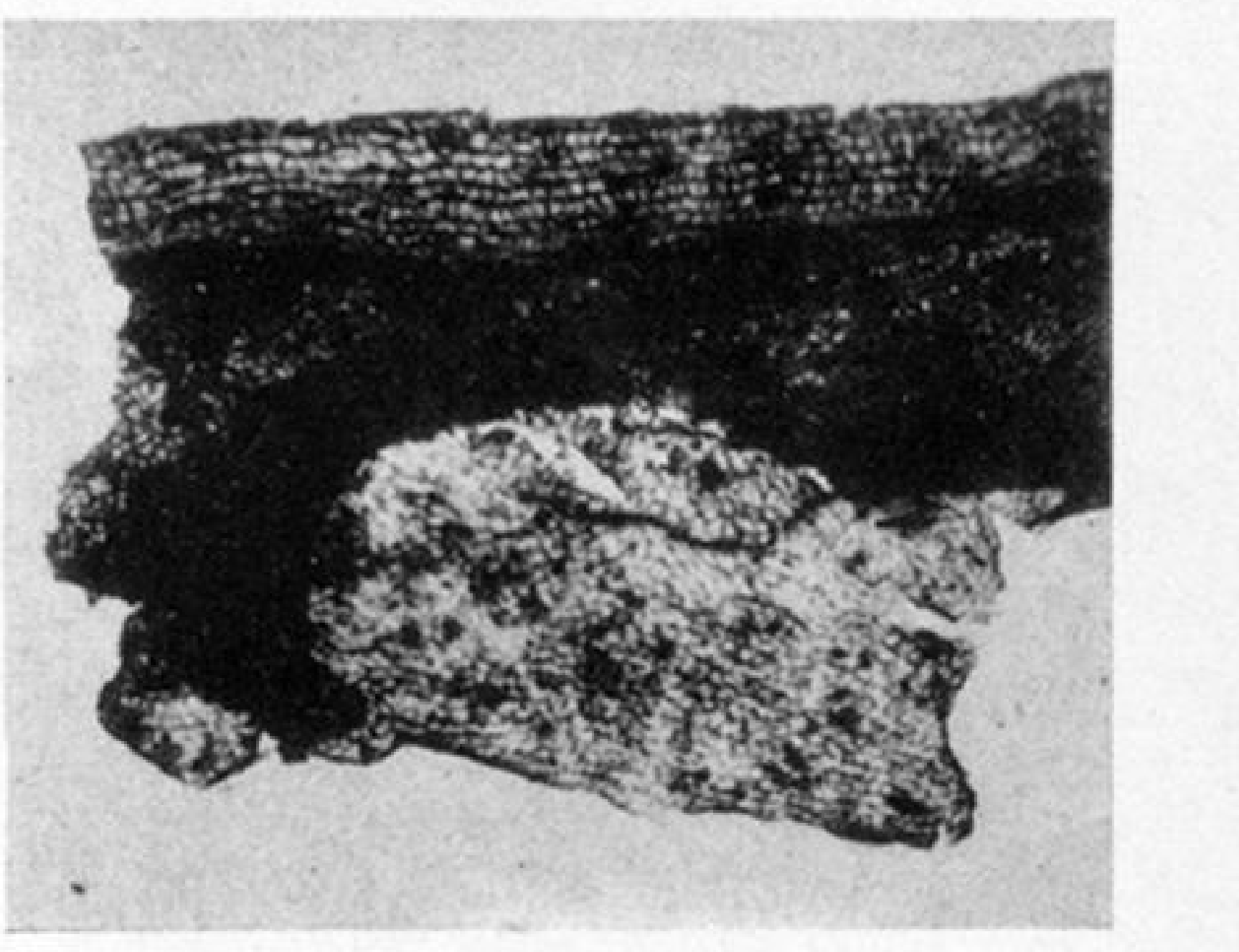
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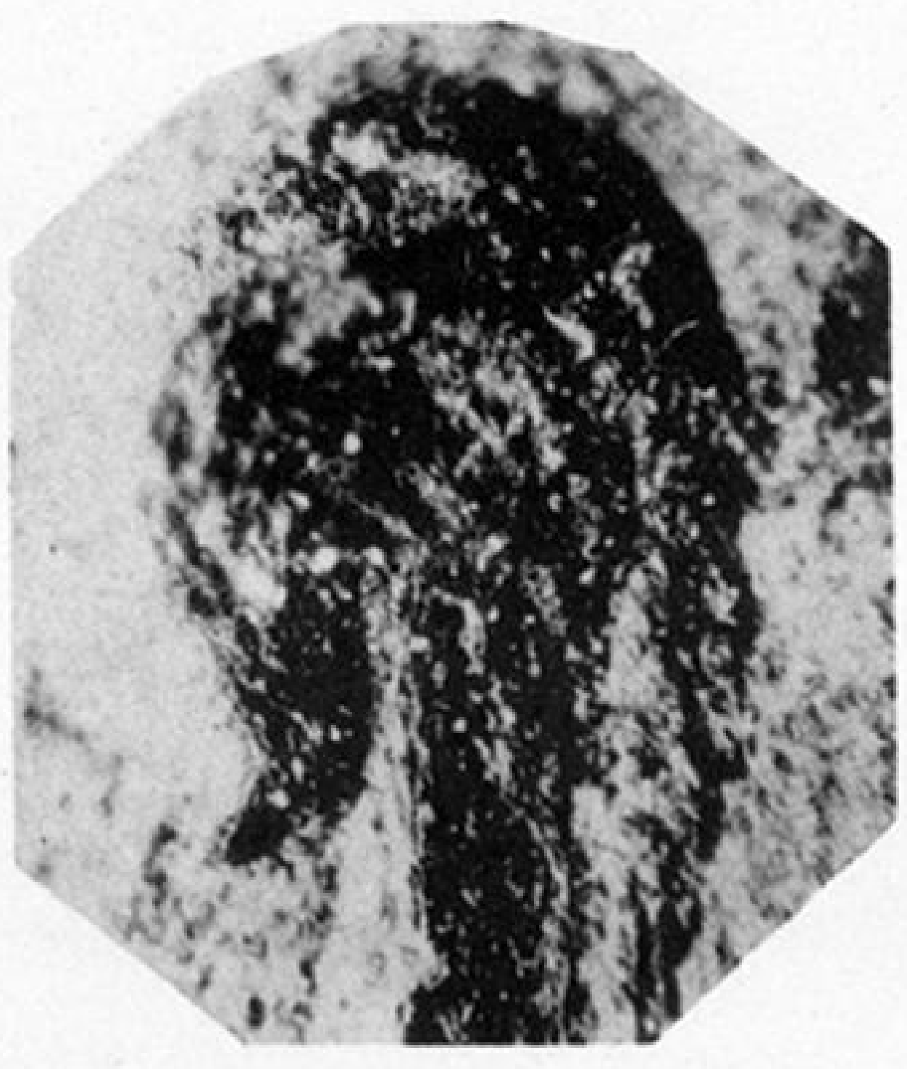
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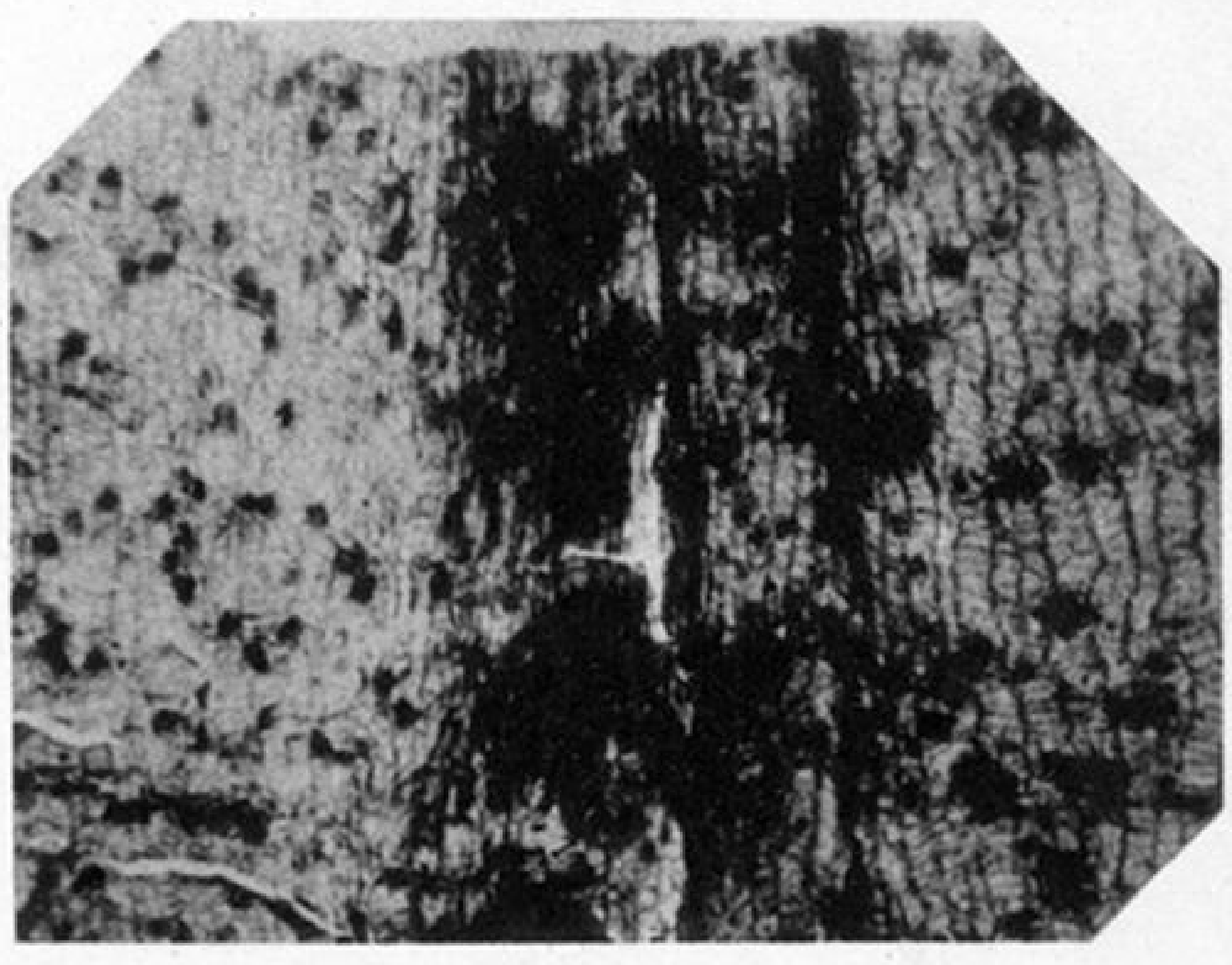
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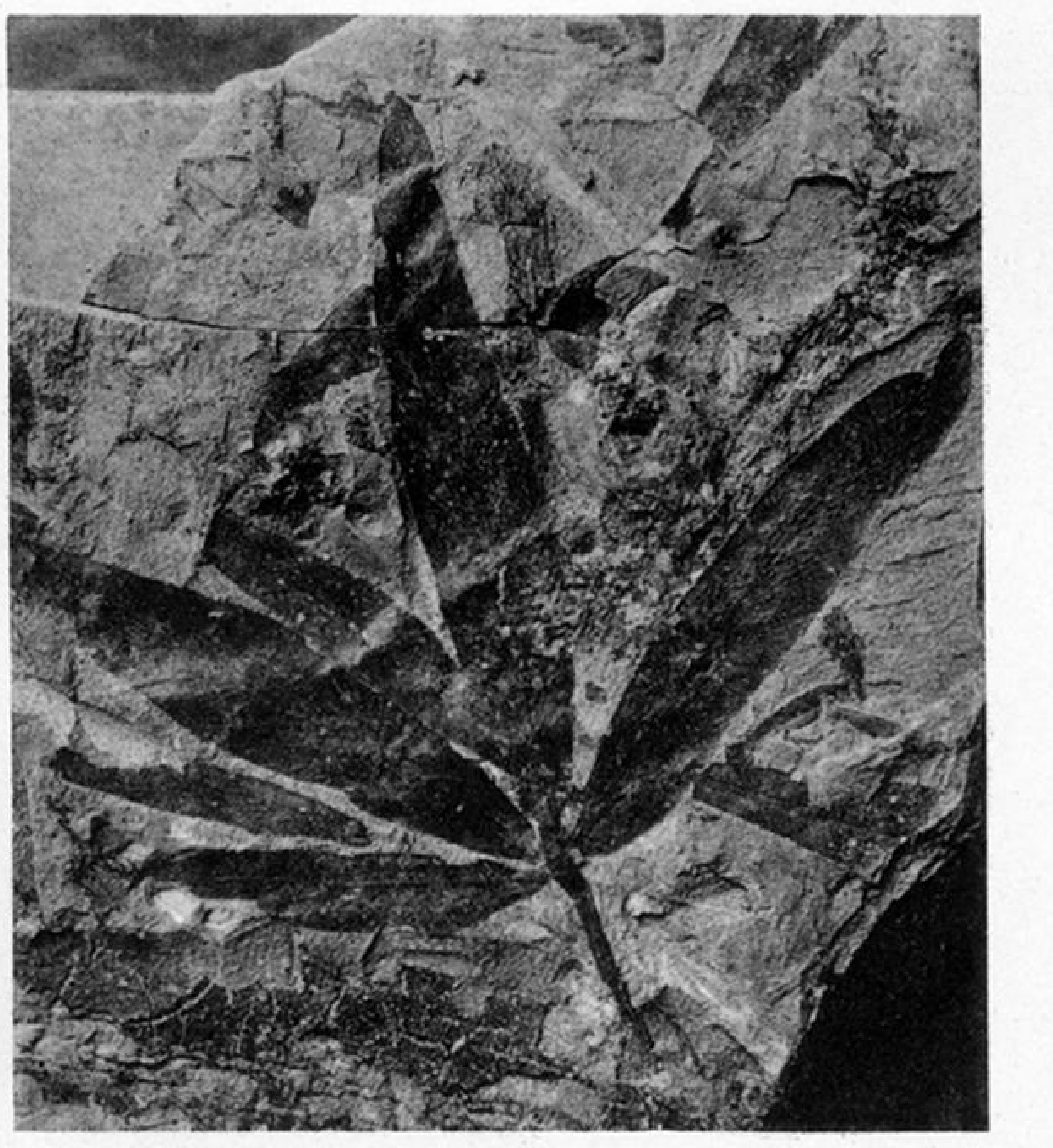
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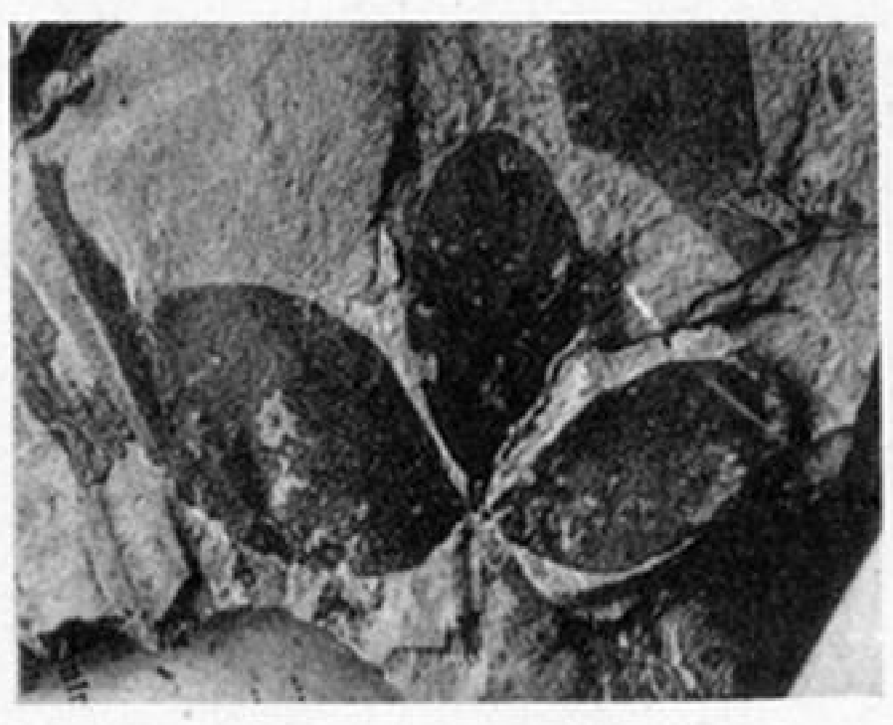
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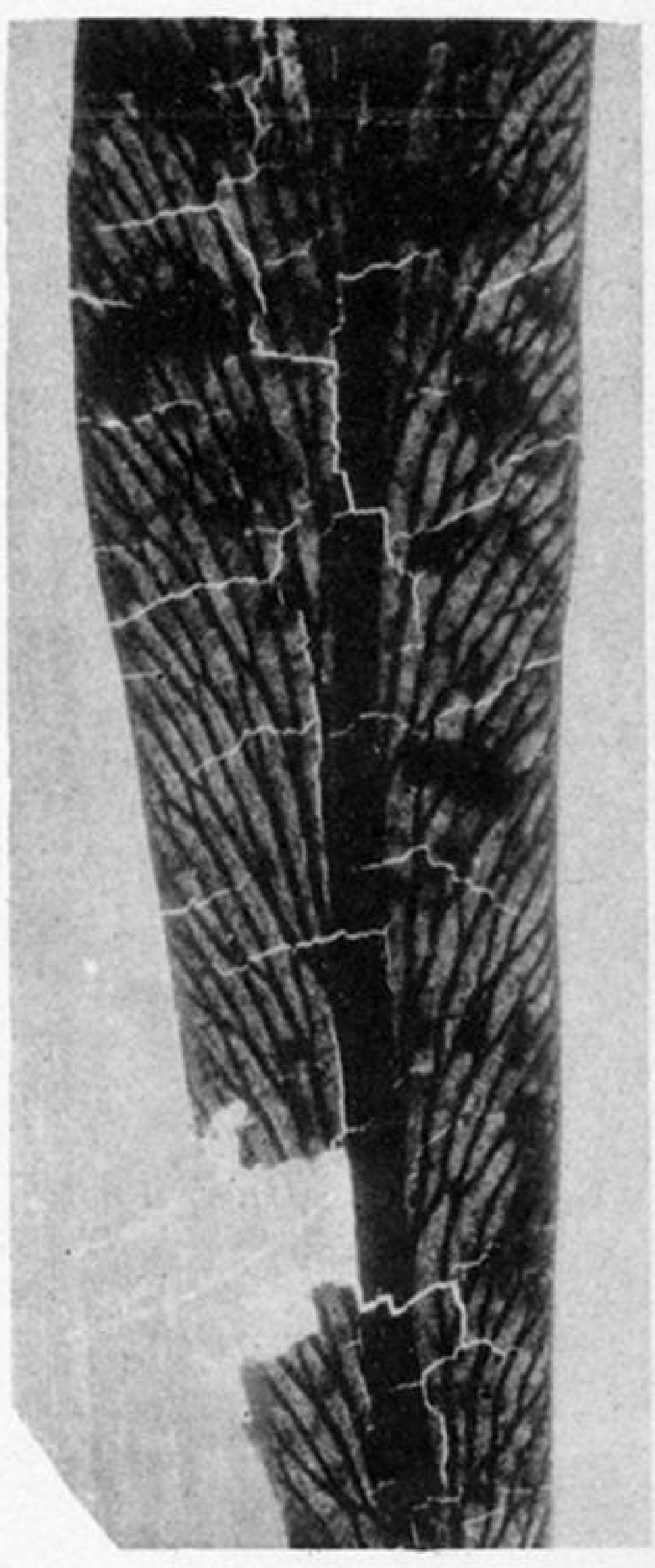
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Gristhorpia Nathorsti and Sagenopteris Phillipsi (Brongn)

PLATE 15.—*Gristhorpia Nathorsti* gen. et sp. nov.

Fig. 43.—Part of a squashed fruit with seeds and small black structures (aborted ovules ?) which appear to have been extruded from it. × 4.

Fig. 44.—Group of seeds and small rounded or oval bodies thought to be aborted ovules, mounted in Canada Balsam and freed from matrix by Mr. J. WALTON'S method. This preparation was made from the counterpart of the specimen shown in fig. 43, and was photographed by transmitted light. × 4.

Fig. 45.—Cuticle preparation of part of the main axis of a young infructescence near a pedicel, showing the difference in the epidermal structure on the upper and lower sides. *Cf.* Pl. 14, fig. 41, and text-fig. 11. × 35.

Fig. 46.—Two young carpels probably from the tip of a megasporophyll. The right hand specimen shows the stigma at the side of the stalk. *Cf.* fig. 47. × 4.

Fig. 47.—The right hand carpel of fig. 46 more highly magnified. It suggests the formation of the carpel from the recurved lamina of the megasporophyll pinna, and the production of the stigma where the tip of the lamina touches the pedicel. *Cf.* text-fig. 2. × 20.

Caytonia Sewardi gen. et sp. nov.

Fig. 48.—Cuticle preparation from main axis of an infructescence (megasporophyll), showing the great difference in the cuticle structure of the two sides and the rounded spots which may be the bases of hairs such as are found on the leaves of *Sagenopteris*. The larger cells of the upper side, shown on the right of the photograph, possess fine projecting points which are not clearly seen at this magnification. *Cf.* text-fig. 12, A, B. × 50.

Sagenopteris Phillipsi (Brongn.).

Fig. 49.—Cuticle preparation from a *Sagenopteris* petiole in specimen CA 10, which was almost indentical in structure with that of a *Caytonia* axis lying near it. The difference in the cells of the two sides are here less pronounced, but the projecting points on the cell walls can be made out. × 65.

Fig. 50.—A typical leaf with four lanceolate leaflets attached to a petiole. Some detached leaflets are also seen. The leaflets have midribs in their lower portions, which die out towards the apex. Cuticle preparations made from petioles of similar specimens have the structure shown in text-fig. 11, C and D. × 3/4.

Fig. 51.—An example of the smaller type of leaf possibly referable to *S. Phillipsi* var. *cuneata*. The three leaflets are small and ovate, with a very short midrib, and the remains of the lamina are very delicate. The structure of the petiole epidermis in this form is similar to that of the axis of *Caytonia Sewardi*. Nat. size.

Fig. 52.—Example of a simple Sagenopteris leaf with no lateral pinnæ, at the apex of a petiole. The petiolar material had been removed for the study of its cuticle. It has no noticeable midrib. Nat. size.

Fig. 53.—Part of a leaflet of the type shown in fig. 50 detached from the matrix and photographed by transmitted light to show the venation. × 4·5.