THE FRUCTIFICATION OF *CZEKANOWSKIA* AND ITS ALLIES

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[Plates 18 and 19]

CONTENTS

Leptostrobus cancer n.sp. is described from well-preserved but broken material occurring in the Yorkshire Inferior Oolite (Middle Deltaic). Its fruiting appendages prove to be two-valved capsules, each valve housing a row of small seeds, probably of inverted orientation and with apical archegonia. The new facts have led to a reinterpretation of *Leptostrobus*, and it is now recognized that the Greenland Liassic fossil *Microcheiris enigma* is the same as *Leptostrobus longus*.

Circumstantial evidence is adduced for referring *L. cancer* to *Solenites vimineus* (also called *Czekanowskia murrayana*) and other species of *Leptostrobus* to other species of *Czekanowskia*.

Leptostrobus, as now understood, cannot be placed in any existing family, but for reasons of convenience no new family is at present instituted.

1. INTRODUCTION

(*a*) *General*

Czekanowskia is a well-known genus of Mesozoic leaves; it is widespread, abundant and has a long range, and it has also been closely studied. It is essentially a genus of isolated foliage, and its other organs have remained obscure. However, like nearly all isolated fossil leaves it has been classified; and strong reasons have been advanced for assigning it to the Ginkgoales and this position has been generally accepted for many years.

This paper provides new information about the fossil cone called *Leptostrobus* and reinterprets the previously described specimens. *Leptostrobus* had been already regarded (by myself) as a reproductive organ of *Czekanowskia*, but so far as I am aware, nobody has expressed views on my arguments. Further evidence is brought forward here to support this contention. *Leptostrobus* is, however, so different from the fructification of *Ginkgo* that it raises grave doubt about the classification of *Czekanowskia* in the Ginkgoales.

(*b*) *The* Czekanowskia *group*

A typical member of the *Czekanowskia* group, e.g. *C. rigida* Heer, consists of bundles of long, slender leaves borne on a caducous short-shoot. The short-shoot bears small-scale leaves, rather as in *Pinus*, but the foliage leaves are ten or more in number, and are distinguished by forking two or three times. The cuticle (known in several species) is similar on the two sides of the leaf. Stomata occur in numerous longitudinal rows, the guard-cells are sunken and surrounded by an elongated ring of rather thickened subsidiary cells. The venation is seldom visible, but there is evidence that the ultimate branches have sometimes a single vein (Florin gives the number as two), and there are two or even as many as four veins locally below a fork. The leaf base, however (which is known from well-preserved, sectioned material), has a single vein which forks below the point of dichotomy of the lamina. Florin (1936*a*, p. 128) has given a very full account of the structure of this leaf, mentioning all the chief species, and the reader is referred to his account for details.

There is unfortunately a difficulty over the name *Czekanowskia*. The first member of this group to be described was a Yorkshire fossil for which Phillips (1829) gave a rough sketch and the name '*Flabellaria* (?) *viminea*'. There was no description. In 1834, Lindley & Hutton gave a slightly better figure and discussed the species at some length; they gave an entirely new name of *Solenites Murrayana*, though they made it clear they were dealing with Phillips's fossil. They thought it allied to *Isoetes*. It is interesting to note that they prepared its cuticle by maceration, and I believe this is by far the earliest preparation made from a fossil. Phillips accepted the change of name without comment in his later work; at that time there was no general acceptance of the rule of priority of nomenclature.

According to rule, *Solenites vimineus* (Phillips) would appear to be the correct name of this plant. The name *Flabellaria* was preoccupied (by a recent plant), but the specific name is valid because although poorly characterized by the figure there is no doubt about its application, since there is nothing else in the Middle Deltaic flora of Yorkshire to which Phillips's figure could refer.

Many years later Heer (1876) described a remarkable series of fossils from Siberia under the new name *Czekanowskia*. He did not identify them with *Solenites*, which he considered too ill-characterized, but he compared them. Subsequent authors writing on the Yorkshire flora identified *Solenites* with *Czekanowskia*, and as Heer's *Czekanowskia* overshadowed Lindley & Hutton's *Solenites* they used the name *Czekanowskia Murrayana* for the Yorkshire fossil. This was the position of Seward who revised it in 1900.

I have recently (Harris 1951) redescribed the Yorkshire fossil under what I regard as its valid name, *Solenites vimineus*. It proves very close to a typical *Czekanowskia*, the only difference being that in *Czekanowskia* the leaf branches at least twice, while in *Solenites* the leaves are, as far as I know, either simple or only once branched. (This branching has been observed in a large number of specimens and is certainly a normal feature, though one easily missed in a leaf over 30 cm. long.) This difference in branching may hardly be of generic importance; but it seems to me that it is convenient to regard it for the present as a generic distinction and to maintain the familiar name *Czekanowskia* instead of sinking it as a synonym of the unfamiliar *Solenites*. In this account, *S. vimineus*, or as others name it *Czekanowskia Murrayana*, is regarded as a closely allied plant to *C. rigida*, and *Czekanowskia* is treated as a sort of subgenus of *Solenites*.

Another genus of this group, *Hartzia*, represented by one species, is only known from the Rhaetic of East Greenland (see Harris 1935, p. 42). It is very like *Solenites vimineus* in its general aspect, but the leaf is slightly broader. It often forks near its apex, but not in its middle region as in *Solenites*. It structure, it agrees closely with *Solenites* and *Czekanowskia*, and if *Czekanowskia* were to be merged in *Solenites* it would be easy to merge *Hartzia* also.

It may be noted that Heer identified some peculiar cones and also some rather ill-characterized seeds with *Czekanowskia*. This is discussed later.

(*c*) Leptostrobus

Heer (1876) described *Leptostrobus* in the same paper as he described *Czekanowskia*. *Leptostrobus* is a genus of remarkably slender cones bearing rather distant fertile appendages above and little scale leaves at the base. Some of Heer's figures are redrawn in figure 1 and they are further discussed on p. 498. No one has ever obtained better specimens of *Leptostrobus*, but Kryshtofovich (1933) figured another good one from Heer's locality. Heer's specimens have been compared with *Voltzia* by several authors.

The next account of *Leptostrobus* was one by Harris (1935, p. 136) on some Greenland specimens which were less perfect than the Siberian ones, but which yielded certain details of structure. They were attributed to *Czekanowskia*, but I did not decide whether *Leptostrobus* produced seeds or pollen. Later (Harris 1937, p. 59) I regarded it as a pollen-producing organ.

In the same paper (1935) I described a small seed-bearing fossil as *Microcheiris enigma*, but this I now believe to be the same as *Leptostrobus longus*. I also described another fossil as *Staphidiophora secunda* (see figure 1), which I now suggest may be a *Leptostrobus*-like organ of *Hartzia tenuis*. The nature of *Staphidiophora* must, however, remain open till fresh material is studied.

The only other additions to knowledge of *Leptostrobus* known to me are the discovery by Oishi & Takahasi (1936, p. 130), Oishi (1940, p. 413), of an imperfect specimen in the Rhaetic of Japan, and another by Turutanova-Ketova (1930) from the Kirghiz.

As will be seen, *Leptostrobus* remains a rare and little-known fossil.

I am unfortunately very imperfectly acquainted with the Russian literature on palaeobotany published since the beginning of the war, but so far as I know no progress has been made with *Leptostrobus*.

The interpretation of *Leptostrobus* in this account is not based, as I would have wished, on one set of specimens supplemented by others but is a structure made by four sets, each by itself inadequate and leaning heavily for support on the others. The four sets are: Heer's original Siberian cones; the Greenland cones called *Leptostrobus longus*; the Greenland specimen called *Microcheiris enigma*; and the present Yorkshire specimens called *Leptostrobus cancer*. I believe I am right in identifying them all generically with one another, but if I am mistaken then a large part of this paper may be groundless. The reader's critical attention is directed to this vulnerable point.

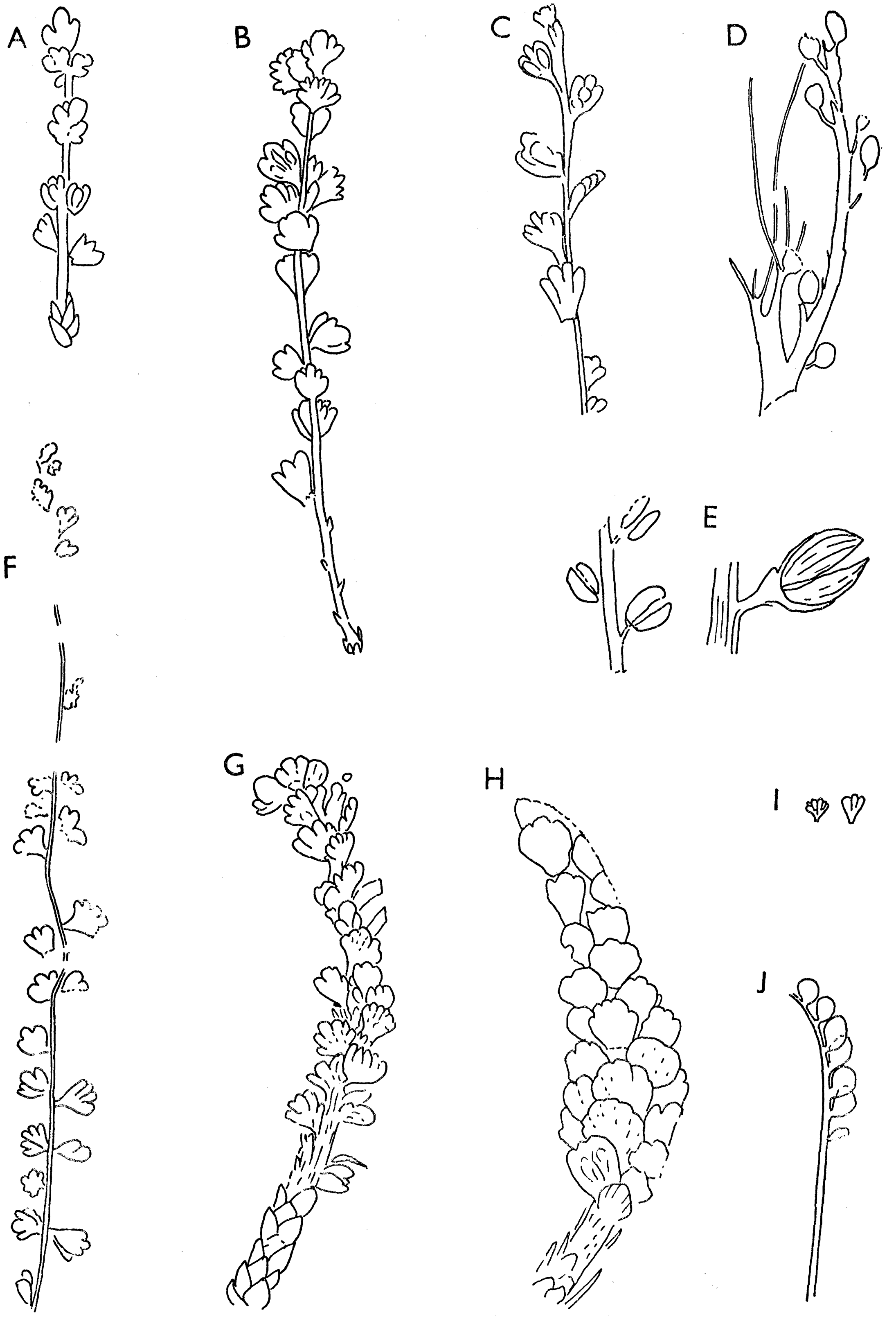

FIGURE 1. Some fructifications which have been referred to the *Czekanowskia* group. The figures are redrawn from the original figures and omit shading and other fine details. A–C, *Leptostrobus laxiflora*. A, Heer (1880, pl. VII, fig. 4). B, Heer (1876, pl. 13, fig. 10A). C, Heer (1876, pl. 13, fig. 1). D, fructification identified by Heer with *Czekanowskia setacea* Heer (1880, pl. VI, fig. 15). E, fructification identified by Heer with *C. rigida*, natural size and enlarged, Heer (1876, pl. 21, figs. 8A and 8C). F, *Leptostrobus longus* Harris (1935, text-fig. 49A). G, H, *L. crassipes*. G, Heer (1876, pl. 13, fig. 14). H, Heer (1880, pl. VIII, fig. 2). I, the two original specimens of *L. microlepis* Heer (1876, pl. 13, fig. 15). J, *Staphidiophora secunda*, attributed to *Hartzia tenuis* Harris (1935, text-fig. 45A).

2. EMENDED DIAGNOSIS OF GENUS *LEPTOSTROBUS* HEER

Seed-bearing fructification consisting of a long and relatively slender axis and small lateral appendages. Base of axis covered with small rounded scale leaves. Middle and upper parts of axis bearing fertile appendages in a loose spiral. Fertile appendage almost sessile, consisting of a somewhat flattened capsule composed of two valves. Capsule as a whole rounded or broadly wedge-shaped and attached by the pointed end; distal margin rounded but marked into about five blunt but more or less conspicuous lobes, lobes continued as more or less conspicuous ridges over the face of the capsule.

Valves convex outside, probably concave within; margins fitting together, but only joined at the base. Seeds about five in number in each valve, one situated under each lobe. Seeds oval, inverted (the micropylar end facing the cone axis) and probably possessing a few apical archegonia. Seeds possessing a cutinized embryo sac, but no other well-cutinized parts; testa of seed imperfectly cutinized, probably composed of a rather thin layer of fibrous tissue.

Cone axis and valves with a well-developed cuticle showing straight-walled cells and numerous stomata. Guard cells sunken in a small pit formed by the subsidiary cells. Subsidiary cell group elongated on the axis, round or elongated on the valve wall. Subsidiary cells often slightly more thickened over their surface than ordinary cells, and with a slight rim of cuticle overhanging the stomatal pit. Encircling cells inconstant.

3. *LEPTOSTROBUS CANCER* N.SP.

(*a*) *Diagnosis*

Cone axis (imperfectly known) probably very slender, bearing fruiting capsules at intervals of about 5 mm. (Cone base unknown.)

Fruiting capsules more or less globose, typically 3 to 5 mm. long, 3 to 5 mm. broad; valves of capsule with feebly developed lobes, distal margin of capsule typically with three to five very obtuse angles forming the lobes but sometimes evenly rounded. Outer surface of valves typically showing three to five broad ridges terminating in the lobes, sometimes evenly convex but substance of valves always with fibrous bands corresponding to the ridges and lobes. Inner surface of valve exposed for a distance of 0·5 to 1·0 mm. inside the margin, and then meeting the opposite valve.

Seeds (? immature) typically 3 to 5 in each valve, elongated, about 2 mm. long × 0·75 mm. broad. (Ripe seeds not known.)

Cuticle of cone axis showing straight-walled cells, stomata occasional, agreeing with the more elongated ones of the capsule.

Cuticle of capsule wall fairly thick (2 to 3 μ measured in folds), of tough consistency. Stomata fairly frequent (20 per mm.^{2}), evenly scattered, not forming files or arranged in bands. Epidermal cells isodiametric polygons, or slightly elongated in the direction of the capsule margin, mostly arranged in rather ill-marked files running from the base to the margin of the capsule.

Lateral walls of cells very strongly marked by a broad, prominent ridge of cuticle; straight but sometimes with very small jagged thickenings. Surface wall of cell typically flat, without a papilla, almost smooth but showing an obscurely mottled surface. Occasional specimens showing either a large, very ill-defined thickening which forms a vestigial papilla; or with a very ill-defined surface sculpture of longitudinal striations.

Stomata well developed, but of rather varied structure. Orientation varied, but often longitudinal. Guard cells sunken in a pit formed by about five to seven subsidiary cells; pit varying from round to longitudinally elongated. Subsidiary cells often forming an

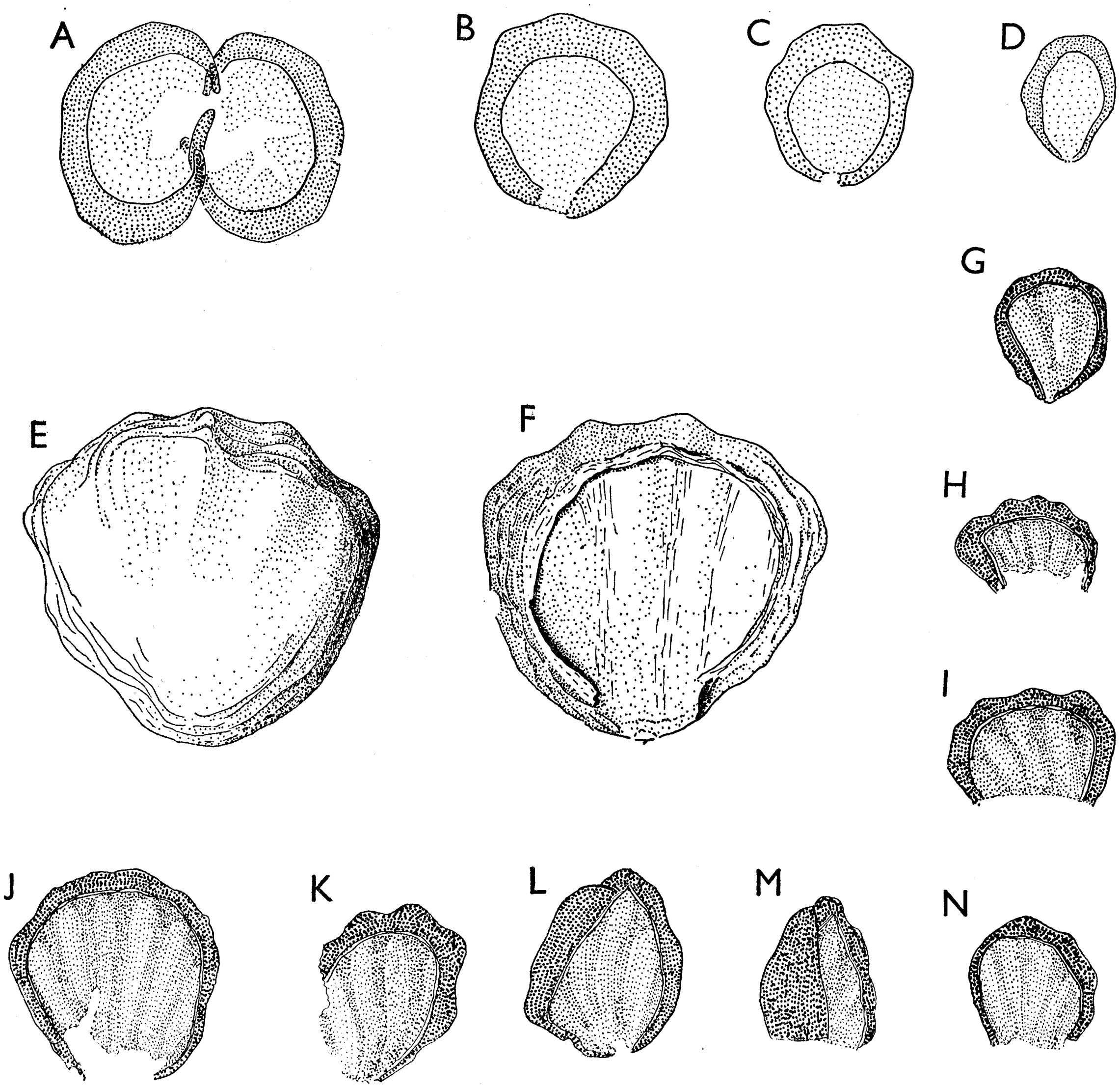

Figure 2. *Leptostrobus cancer* capsules. A–D, fully macerated cuticles, all at magn. × 5, with the infolded margin stippled darker than the valve face. A, the two valves of one capsule teased apart, the valve on the left has the thicker cuticle, slide V 28564. B, slide V 28565, also figured in figure 3G. C, slide V 28566. D, exceptionally small valve, slide V 28567. E, type specimen outside of valve seen as an opaque object, as originally exposed. F, inside of same valve in balsam transfer. This specimen is also figured in figure 16, plate 18, and figure 23, plate 19, V 28568. G–N, series of valves unmacerated or only partly macerated and viewed by transmitted light to show the darker ribs. All at magn. × 5, slide V 28567. The specimen in G is unusually small, those in L and M are exceptional in being obliquely compressed.

elongated group, but terminal subsidiary cells undifferentiated or only slightly differentiated. Subsidiary cells with slightly thicker surface than the other epidermal cells; usually forming a rim constricting the stomatal pit; pit either round and evenly constricted or elongated and rim better developed at the sides than ends of the pit. Encircling cells inconstant, but majority of stomata with some encircling cells, or even with a complete set. Exceptional stomata showing two rings of encircling cells. Encircling cells usually resembling other epidermal cells in thickness. Trichomes absent.

The specific name is from *cancer*, a crab, suggested by the resemblance in shape of the isolated valve to an empty shell of a crab (see, for example, figures 2 E, F).

(*b*) *Description*

Material

The material consists of a few blocks of shale collected by me in 1945 from the Cloughton Wyke Solenites Bed (the classic Cloughton locality) and three old blocks in the York Museum, the matrix and flora of two of which almost certainly indicate their origin from the Cloughton Solenites Bed also. The third York specimen, preserved in what appears to be typical Gristhorpe Bed matrix, is labelled $\frac{60}{2{\cdot}236}$ and mounted on a card labelled 'Middle Estuarine Series, Loc. near Scarborough, Sp. *Beania* (*Sphaereda*) *parvula*, Bean'. It bears three isolated capsules, one of which was macerated.

One of the York specimens attributed to Cloughton seems to be the original of Phillips (1829, pl. 7, fig. 25). This block bears the following labels:

Sphaereda parva Bean
Lower Shales Scarborough
Unknown leaves Phillips
Pl. 7, fig. 25.

It has a small red circle denoting a figured specimen.

Another label just gives 'W.R.'

The other York block is labelled 'small vegetable leaves of Phillips, pl. 7, fig. 25. Lower shale Scarborough'.

The name *Sphaereda parva* is, I imagine, a spelling variant of *S. parvula*, one of Bean's many *nomina nuda*. One York Museum specimen labelled *S. parvula* proved quite different; it shows round bodies of the same size as the present capsules which proved to be coprolites full of *Caytonanthus* pollen (Harris 1946).

Both these York specimens and also the ones collected by me show numerous isolated capsules of *Leptostrobus* scattered over one side of the block. In my own specimens they are not strictly confined to one bedding plane, but were proved to occur in considerable numbers throughout a thickness of about 5 mm. of rock, but none were seen at other levels. Some fifty or so capsules are exposed on the rock faces, but most of them are rather damaged. About another hundred capsules were obtained by dissolving the rock matrix in hydrofluoric acid, but while most of these again were damaged, either during preservation or in preparation, a fair number of excellent specimens were recovered. The cuticle of the capsule is fairly tough and, with care, can be prepared intact.

Cone axis

No cone axis is preserved on the surfaces of any of the slabs of rock.

When the matrix was macerated, search was made for fragments of cone axes and three such were found. All three seem to have rotted a good deal before preservation, and very little internal substance remained enclosed by the cuticle.

The largest piece was very crushed and dilapidated; it is 1 cm. long and about 2 mm. wide, though its true width is doubtful owing to folds which were torn in preparation. It shows three, or possibly four, scars where appendages have been torn off; they occur on all sides, but it is impossible to make out the phyllotaxis.

Two other fragments are better preserved and are both just over 1 mm. wide. One has one scar (figure 25, plate 19) the other has two.

The 'scars' consist of an extension of the axis in an outward and forward direction. The cuticle is torn in a ragged manner from the axis. There is nothing to show whether the appendage was lost before preservation, or broken off during extraction from the rock, but the irregular outline of the cuticle suggests accidental tearing rather than neat abscission.

The axis has a cuticle of medium thickness which is tough and easy to handle. It is composed of elongated cells with more or less oblique ends. The walls are straight and strongly marked; some of them show a slight suggestion of jagged thickenings. The surface wall is flat and not papillate, the surface sculpture is of very fine mottling. Stomata are rather sparse, between 10 and 20 per $mm.^2$, and some of them seem poorly formed. They are scattered (not forming rows) but are all longitudinally orientated. The guard cells are sunken, the pit is narrow and formed by an elongated group of subsidiary cells. The subsidiary cells are either of just the same thickness as the rest of the epidermis or very slightly thickened, or occasionally slightly thinner. They bear no papilla on their surface, but a cutinized rim overhanging the margins of the stomatal pit. Encircling cells are variable, sometimes absent, sometimes forming an almost complete ring, but are never specialized.

A very few simple trichomes occur on the axis. Each consists of a tubular prolongation of the cuticle of an epidermal cell; typically 100 μ long and 25 μ broad.

The pieces of axes are identified with the fruits because:

(1) they are associated with the fruits,

(2) they are very like the axis of *Leptostrobus longus*,

(3) the scars of the missing lateral appendages are similar in size to the break at the base of the *L. cancer* fruits,

(4) the cuticle in general and the stomata in particular are similar but do not resemble those of any other associated plant.

The capsules

About half the capsules have their two valves intact; the others are represented by separate valves. The valves themselves did not break up before preservation (but were often broken during extraction from the rock).

The capsules shown in plate 18 are of normal size and shape. None is appreciably larger than this, but a good many are smaller. The smallest seen measured 2·5 mm. long and broad; such specimens are imagined to be starved capsules at the top of the axis.

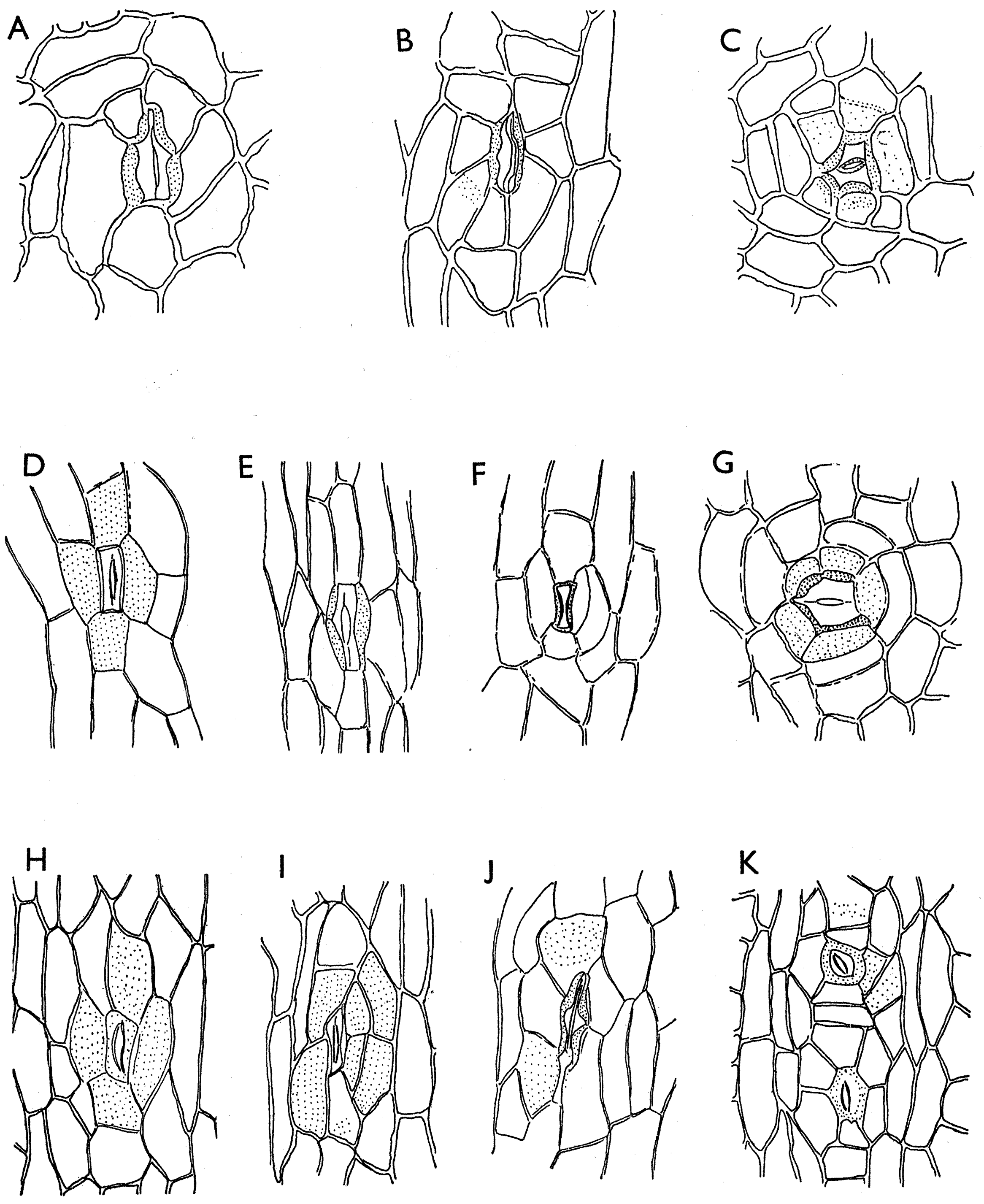

FIGURE 3. Stomata of *Leptostrobus* spp. and of *Solenites*, all at magn. × 400. A–C, *L. cancer*, three types of stomata from the same valve, all being frequent and within the range of the 'normal', V 28569, also shown in figure 20, plate 19. D, *Leptostrobus longus* typical stoma from valve, Greenland collection slide 2821. E, F, *L. cancer*, two stomata on the cuticle of the axis, V 28570. G, *L. cancer*, stoma with numerous encircling cells from a specimen in which an unusual number of stomata are of this type, V 28565 (also shown in figure 2B). H–K, stomata of *Solenites vimineus* from specimens associated with *Leptostrobus cancer*. H, I, stomata of the commonest type. J, exceptional stoma. H–J, all from V 28592. K, two stomata, the upper of very unusual type, specimen also figured in figure 27, plate 19, V 28591.

Typical valves are about as long as broad, and often nearly round in outline. A few are slightly longer than wide, and others slightly wider than long, and there is no reason to suppose that these forms are caused by distortion, but a good many others are distorted and owe their unusual shapes to unusual planes of compression. Such specimens suggest that the valve was a little flatter than hemispherical, making the whole capsule nearly globose. Where the two valves are still present they usually fit together (figures 11 and 17, plate 18) but not closely enough to exclude rock matrix; the specimen shown in figure 12, plate 18 where they diverge is exceptional.

The capsule illustrated in figure 2A shows a difference in thickness between the cuticles of the two valves, though their cells are similar. Other specimens may also show such a difference, but this is less marked.

The figured specimens illustrate the variation in the shape of the valve margin. The commonest form is one where the distal margin has three to five obtuse angles. Specimens in which the 'angles' are extended to form distinct bulges are common and also some where the angles are almost suppressed so as to give an evenly rounded outline to the valve.

The surface of the valve usually shows a series of obscure broad ribs running to the marginal 'angles'; these ribs too are variably developed and occasionally are obscure. Even where the surface is smooth the position of the rib is often made obvious by colour, the rib being thicker and black, the intervening space thinner and brown. The only specimens showing no sign of the ribs are those which have suffered complete natural (or artificial) maceration and nothing but cuticle remains. Specimens which have suffered a moderate amount of natural maceration often show the distal end of each rib as a conspicuous dark patch, when the rest of the rib has disappeared.

Specimens compressed in unusual planes suggest that the ribs were originally much more prominent than they are in the compressed fossil. The presence of little compression folds in the cuticle along the sides of the ribs points the same way.

The substance of the wall of the valve is just thin enough to transmit light in the best specimens. In the better specimens the valve seems to be lined with a hypodermis of cells about $40 \times 40\,\mu$. There are oval gaps in this layer, probably above each stoma. This layer is supplemented (or possibly replaced) by elongated cells along the ribs; it was not possible to make out the ends of these elongated cells, but they suggest fibres. At a rather deeper level there is an incomplete layer of large oval cells $50 \times 60\,\mu$ which are evenly scattered in the areas between the ribs. Their walls are thick, and they are regarded as sclerids or isolated stone cells.

No other cell layers are recognizable in the unmacerated valve, but it is possible that there were a good many layers of delicate cells forming a soft tissue.

The base of the valve is irregularly broken and often shows a large gap. In the best specimens the outer surface of the valve is almost unbroken, but a piece of the marginal flange is missing. As a rule there is an irregular tear at the base of the outer wall of the valve as well.

Marginal flange

The marginal flange is the part of the valve which faces the opposite valve in the intact capsule. The flange is typically about 0·6 mm. wide in the distal region and grows narrower, about 0·3 mm. wide near the base. At the base it is always broken away. The substance of the margin appears to be a little less massive than the rest of the valve wall, and the fibrous layer of the ribs may not continue into it; it was, however, difficult to obtain evidence, as much of the marginal flange is fused to the rest of the valve. Near the free edge of the flange the substance suddenly becomes delicate.

The angles or lobes of the margin were carefully examined to see if there was any kind of opening here. There is not; on the contrary, the cuticle is slightly better developed here than elsewhere.

The seed

The seed of *L. cancer* is ill known; very few of the capsules show any trace of seed, and even these may be unripe or abortive specimens.

Figures 5 to 8, plate 18, show two valves in which pieces of the chalazal ends of seed are present, though much has been broken away, probably in preparation. Each seed is connected by a dark strand to the tissue beneath a lobe of the capsule, and each seed shows a dark inner mass (the megaspore membrane) surrounded by an integument-like layer which on maceration proves to be the 'fibrous membrane' described below.

A few capsules are closed and contain no rock matrix; and these always show many seeds, but they are so delicate that they are usually broken in small pieces. In figure 26, plate 19, the dark matter behind the margin proved, under different lighting, to consist largely of the chalazal ends of megaspores, while the less dark part below this is chiefly broken pieces of the 'fibrous membrane'. Figure 10, plate 18, shows a nearly intact but very small megaspore membrane dissected out of such a capsule; as a rule the megaspore membranes seem to be 1·0 to 1·5 mm. long.

The specimen in figure 26, plate 19, is not quite fully macerated. It is unusual in that all its megaspore membranes are of small size, well under 1 mm. long. Below some, and perhaps all, of the megaspores there is a small dark nodule very like the pollen masses of the specimen called *Microcheiris*. Accordingly, it was removed and further macerated, and it was proved that each was in fact a pollen mass. One of these masses teased out from the capsule is shown in figure 24, plate 19, and in figure 4B; the others are similar or a little larger, but the pollen grains composing these masses are so numerous and so compacted together that it is not possible to trace the outline of any one of them completely.

The innermost layer of the capsule which is called the fibrous membrane proved troublesome to investigate and is by no means understood. After maceration it consists of a soft material showing very dimly the outlines of several layers of cells. The fibrous membrane forms a sheath round the chalazal ends of the seeds just as an integument would do, but it also extends far beyond the apices of the embryo sacs down to near the base of the capsule, as though it here forms the inner lining of the capsule. The scattered pollen grains in the capsule are all sticking to this layer.

It is supposed that the fibrous membrane represents several layers of cells which have been preserved because of a slight fat impregnation. It is certainly associated with the seeds because most of the capsules have lost their seeds and have lost their 'fibrous membranes' also, but its position and nature is left open.

The megaspore membranes of *Leptostrobus cancer* vary in size, but are nearly constant in fine structure. They were repeatedly proved to be a double membrane (a collapsed sac) and the two surfaces, though very close, are not fused together, so there must be a little soluble matter between them. There is some variation in different parts of a single megaspore in the folding of the surface and in the density of granules; that in figure 9, plate 18, shows conspicuous folds and few and therefore distinct granules. The folds sometimes look just like cell outlines; but often they cross one another, and it seems likely that none of them are true cells.

After archegonium-like cavities had been found in the apices of the megaspores o '*Microcheiris*' a search was made for similar ones in the megaspore fragments in *Leptostrobus cancer*. No convincing example was found, but the occurrence of pollen masses in the specimen shown in figure 26, plate 19, in the same position as those of '*Microcheiris*' indicates that the seeds are inverted here also.

It is unfortunate that the seeds are so imperfectly known. The rock matrix was searched for isolated seeds of suitable structure but none was found.

Pollen grains in the capsules

None of the present specimens is as richly provided with pollen grains as the Greenland ones (especially '*Microcheiris*'), but all those that still possess the fibrous inner membrane show moderate numbers of grains scattered over it. The specimen shown in figure 26 has, in addition, several compact masses of pollen situated just below the embryo sacs, in positions which correspond with those of '*Microcheiris*', and there are similar pollen masses among the broken fragments from inside other specimens. It is very difficult to make out the form of the pollen grains in these masses as they overlap; the only thing certain is that there are many large grains, some about 50 μ wide, with rather thin, very finely punctate walls. I am not able to say whether wings and triradiate scars are absent, but I could see none.

Around these pollen masses there are scattered pollen grains which can be observed better; some of these are large oval grains up to 80 × 50 μ with longitudinal groove, and others roundish grains about 35 μ wide, also with a longitudinal groove. I did not recognize any winged pollen grains at all, but I saw a few thick-walled grains looking like fern spores.

I feel certain that these pollen grains are of more than one species. In the Greenland specimens there was much greater variety in pollen, including at least the following four kinds, all of them abundant:

large winged grains	130 μ × 80 μ
large oval grains	90 μ × 60 μ
smaller oval grains	35 μ × 30 μ
round grains	30 μ diameter

In view of this variety one would hesitate to suggest that any particular kind belonged to *Leptostrobus*. Clearly, however, the probable absence of winged grains in *L. cancer* is rather against my former idea that the winged pollen belonged to it.

(*c*) *Comparison of* Leptostrobus cancer *with other species of* Leptostrobus

The other named species of *Leptostrobus* (cones) are *L. laxiflora*, *L. crassipes* and *L. microlepis* from Siberia and Russia, *L. longus* from east Greenland, and there is an unnamed specimen resembling *L. longus* from Japan. Of these, *L. microlepis* is too ill-known for comparison; it might be an ill-developed *L. laxiflora*; Kryshtofovich & Prinada (1934) omit it from their list.

L. cancer has a slender axis like *L. laxiflora* and *L. longus*, but both of those species differ in their strongly lobed capsules. *L. crassipes* (with a thick axis) has capsules which agree in their feebly developed lobes and surface ridges, but they are usually much larger.

L. longus, the only other species whose structure is known, has a very similar cuticle indeed. The cuticle of the axis of the two species is at present indistinguishable; it is true that no trichomes are known on the axis of *L. longus*, but they are so rare in *L. cancer* that they can hardly be used as a distinguishing character. The cuticles of the capsules, though very similar are, however, distinguishable; *L. cancer* has as a rule smaller, thicker walled cells (30 to 40 × 25 μ) than *L. longus* (70 to 80 × 40 to 50 μ). In *L. longus* the stomatal apparatus of the capsule nearly always has an elongated pit, but in *L. cancer* it is very often rounded.

The inner (fibrous) membranes of the capsules in the two species, and their megaspore membranes, are at present indistinguishable.

4. REVISED DESCRIPTIONS OF ALLIED SPECIMENS

(*a*) *The Greenland specimens called* Leptostrobus longus

(Harris 1935, p. 138, pl. 7, figs. 1–5, 11–17, ? figs. 6–10, ? pl. 24,
fig. 8, text-fig. 49, text-fig. 50 I)

I have not examined the hand-specimens again. They were only indifferently preserved, and were made rather worse through my efforts to work out their structure by maceration. They are in the collection of the Geological Survey of Greenland at Copenhagen.

I have, however, re-examined all the preparations of cuticles, and while I can confirm most of what I previously stated, certain facts are now recognized for the first time and my account is corrected. I had supposed that the lateral organs were originally cup-shaped. This was a mistake; one of the preparations (2881) shows the lateral edge of a valve though this feature was missed. Accordingly, a new restoration is given here.

The inner membrane of the capsule wall was barely mentioned, but search showed a few fragments of a layer agreeing with the peculiar ‘fibrous membrane’ of *L. cancer*. Various kinds of pollen grain occur sticking to this membrane.

(*b*) *The Greenland specimen called* Microcheiris enigma

(Harris 1935, p. 118, pl. 8, figs. 5–6)

This specimen is important because it gives the best picture of the valve of *Leptostrobus longus* and because it shows certain features even better than *L. cancer*.

The single specimen was obtained by maceration of shale and was fully cleared when found. It is re-illustrated here because, being now better understood, it can be followed more closely.

The specimen is a small scale or valve nearly 6 mm. long × 5 mm. broad. Its base is broken and the top is divided into five blunt ‘fingers’. As mounted, it consists of cuticle only, and has been severely crushed in preservation; the cuticle shows many compression folds round the margins and elsewhere.

The cuticle of the outer side continues over the lateral margins and around and over the fingers and then changes abruptly on the inner side at a distance of about 1 mm. from the distal margin and becomes very delicate and is largely missing. This delicate extension overlaps the distal ends of the seed megaspores. Apart from this, no cuticle remains over the seed megaspores, but comparison with *L. cancer* suggests that the 'fibrous membrane' occurred here but was lost in preparation.

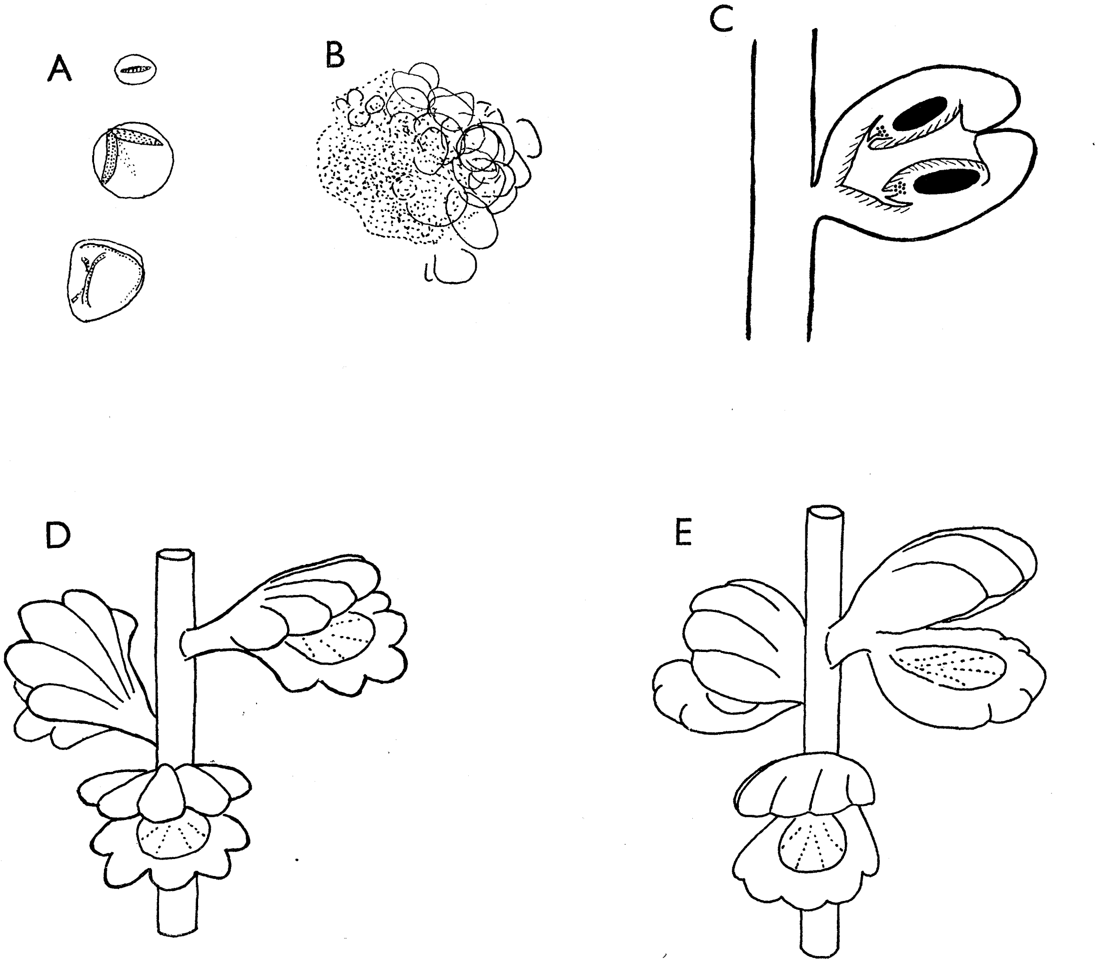

FIGURE 4. A, three pollen grains or spores of unknown origin adhering to the inner cuticle of a capsule, V28580. (Magn. × 200.) B, pollen mass dissected from below a seed megaspore. Only the more obvious grains are indicated, the stippled matter shows no distinct structure (shown also in figure 24, plate 19. V28578. (Magn. × 100.) C, restoration of *Leptostrobus* capsule in L.S. The megaspore is shown in solid black, the inner fibrous cuticle is cross shaded and the pollen grains are shown as black dots. The micropyle of the seed is entirely imaginary. (Magn. × about 5.) D, restoration of part of a *Leptostrobus longus* cone. (Magn. × about 5.) E, corresponding restoration of part of a *L. cancer* cone. (Magn. × about 5.) In D and E the morphological apex of the cone is shown upwards.

The rest of the inner face of the fossil is covered with a very delicate and fragile membrane (the fibrous membrane) which has a considerable affinity for strain. It has cracked into little rectangular blocks, many of which are missing. It shows no clear cells at all, but only faint and obscure striations suggesting a mass of crushed fibres rather than an epidermis.

The relations of this delicate fibrous layer to the cuticle at the margin of the valve could not be made out.

There is an embryo sac below each 'finger' or 'lobe'. These sacs are crushed flat, but the upper and lower sides can be recognized as non-cellular membranes covered with small granules which are irregularly united into irregular lumps. Nothing remains inside the embryo sacs.

The apex of each embryo sac points towards the base of the scale and is emarginate, as though either strongly depressed, or else slightly torn at this point before preservation. In addition, four of them, and perhaps the fifth also, show a small round gap at this end about 40 μ wide which I interpret as the opening for an archegonium neck; one of them gives an indication of a second of these gaps. No such gaps occur in any other part of the embryo sac.

Above the chalaza of each embryo sac there is a faint and ill-defined dark patch, due to a little darkly stained matter in this region, but this matter reveals no definite cells, but only very obscure striations.

The inner cuticle of the valve is thickly covered with pollen grains though these are of several types, and their distribution is very uneven. In the distal region they are very few indeed, barely as many as 1 per mm.^{2}, and there are probably none at all sticking to the cuticle of the outside of the valve. They become numerous, however, on the inner sides of the base of the valve where the number reaches about 60 per mm.^{2}; and the concentration increases on the inner face of the valve below the bases of the seeds where the grains are more or less in contact or overlap. Finally, at a point 0·3 mm. below each seed there is a solid compact mass of pollen, each mass consisting of perhaps 100 pollen grains. No tissue is preserved connecting these pollen masses with the embryo sacs, but there is a suggestion of a core in each pollen mass and there is also a suggestion that the pollen masses are not quite shapeless but slightly moulded into a cone. These masses must owe their existence to some original structure in the valve, and while it may be imagined that the pollen is situated at the bottom of a micropyle in a nucellar pollen chamber, there is no trace of these parts.

It was noticed that a few pollen grains occur beneath the edges of the embryo sacs, especially in their apical regions, and this seems to show that there was originally a gap between whatever tissue surrounded them and the wall of the valve, but this gap did not extend far.

In my account I regarded *Microcheiris enigma* as a flattened, seed-producing organ, as indeed I do now, and I regarded the capsule of *Leptostrobus longus* as a radially symmetrical organ of entirely different nature. I did not discuss their identity. It was only when *L. cancer* was investigated, a fossil which showed obvious resemblances to each, that the possibility was first considered; it was then confirmed by re-examination.

'*Microcheiris*' is the same size as the 'cup' of *Leptostrobus longus* and is divided very similarly into lobes. Its axis is unknown, but the cuticle of the valve can be compared. That of '*Microcheiris*' is slightly more delicate and is somewhat shrivelled, showing many small folds which are not original since they cross cells irregularly. The epidermal cells themselves are identically similar. A feature which was missed in '*Microcheiris*' is that the cuticle continues over the margin and then abruptly ends (or becomes very delicate) just as in *Leptostrobus longus* (and in *L. cancer*).

Stomata are difficult to find on the valve of *Microcheiris* and were reported absent. The specimen is mounted with the inner side upwards, and in any case the cuticle is much folded. Search has, however, revealed some stomata; their subsidiary cells are like those of *Leptostrobus longus* but less thickly cutinized.

I think the difference may be all due to immaturity of '*Microcheiris*' which would account for the presence of young seeds, thinner cuticle and wrinkled surface. The specimens called *Leptostrobus longus* are full grown and empty husks.

The generic identification of '*Microcheiris*' with *Leptostrobus cancer* is based on strong evidence. Besides the general agreement in shape with *L. cancer* valve we have: agreement in the extent of the outer cuticle of the valve (extending over the lobes and then stopping abruptly); agreement in the very remarkable inner cuticle of the valve; agreement in size and character of the megaspore membranes; agreement in the position of the pollen masses.

The value of '*Microcheiris*' is in the light it throws on the other specimens of *Leptostrobus longus* and in the information it gives about the number and position of the seed megaspores, and their associated pollen masses.

(*c*) *The specimen called* Staphidiophora secunda

(see Harris 1935, p. 114, pl. 8, figs. 3, 4, 9, 10, 11; text-fig. 45)

A single specimen of this fructification was found associated with *Hartzia tenuis*, and was identified with it because it has similar stomata. The specimen is redrawn in figure 1; it is seen to be rather like *Leptostrobus* except in the secund arrangement of the appendages; but this results from twisting of the axis.

The appendages were macerated and yielded the cuticle fragments I described, and it was concluded that the lateral appendages were seeds. This interpretation is possibly correct, but an alternative which is now realized to be possible is that the appendages are capsules containing a number of small seeds. This can only be settled by the study of further specimens; but it is clear that just as the leaf *Hartzia* agrees closely with *Solenites*, the fruits attributed to the two may be closely similar.

The small fossil described by me as *Staphidiophora* (?) *exile* (Harris 1935, p. 116) is too little known to be discussed here.

(*d*) *Notes on Heer's Siberian specimens of* Leptostrobus *and the fructifications attributed to* Czekanowskia

(*Leptostrobus laxiflora* Heer 1876, p. 72, pl. XIII, figs. 10–13; pl. XV, fig. 96;
Heer 1880, p. 23, pl. VII, figs. 1–5)

Heer's figures (see figures 1A to C in this paper) represent excellent specimens which may well form a true species, but their botanical nature is obscure. The drawings suggest a variety of different seed arrangements, and I would suggest that bodies he regarded as seeds are true seeds but are seen as bulges through the capsule wall.

Leptostrobus crassipes Heer may be divisible into two groups, one with 'scales' or capsules the same size as in *L. laxiflora* (Heer 1876, pl. XIII, fig. 14; 1880, pl. VII, fig. 7; pl. VIII, figs. 4, 5); the other has larger 'scales' with an entire margin (pl. VIII, figs. 2, 3). One specimen (1880, pl. VIII, fig. 1) links the two groups. A point of considerable interest is that in his 1880, pl. VIII, figs. 2 and 3, the 'scales' imbricate in a phyllotactic spiral. This indicates that they are approximately in their true position and are vertically flattened as Heer supposed, and if they are composed of two valves, then one valve is above the other.

Leptostrobus microlepis Heer, 1876, p. 74, pl. XIII, fig. 15, 15*b*, 15*c*; 1880, p. 25, pl. VII, fig. 6, is ill-characterized and may be the apical part of *L. laxiflora.*

Leptostrobus rigida Heer, 1880, p. 25, pl. VII, figs. 11, 12; pl. VIII, figs. 1*b*, 5*b*; and *L. angustifolia* Heer, 1880, p. 26, pl. VII, figs. 8–10, are the names of elongated leaves in bundles, rather closely resembling *Solenites vimineus.*

Fructification attributed to Czekanowskia rigida (see Heer 1876, pl. XXI, fig. 8, redrawn in figure 1E). This fossil looks as though it may possibly be of *Leptostrobus* nature, but it could equally well be an axis bearing paired seeds as Heer supposed. Its reference to *Czekanowskia* seems to be suggested by its *Ginkgo*-like appearance.

Fructification attributed to Czekanowskia setacea (see Heer 1880, pl. VI, fig. 15, redrawn in figure 1D). I think it unlikely that this fossil belongs to *Czekanowskia* at all, as the leaf-like appendages are so differently attached.

5. Evidence of attribution of *Leptostrobus* to *Czekanowskia*

The evidence of attribution is:

(1) association, repeated for several localities and different species of different ages,
(2) agreement in structure.

General position

It is curious that Heer never discussed the possibility that *Leptostrobus* might belong to *Czekanowskia*; he decided that *Leptostrobus* was a *Voltzia*-like conifer while *Czekanowskia* was the foliage of a *Ginkgo* ally, and this being so they could have nothing to do with one another. The fact that *Leptostrobus* bears little leaves at its base, looking very like the foliage leaves of many conifers, was part of Heer's evidence. These scale leaves might, however, have been taken as evidence that *Leptostrobus* does not belong to a plant with shoots bearing such scale-like leaves, since no such conifer occurs with them.

In a later paper he regarded some narrow pine-like leaves as the foliage of *Leptostrobus*, and in view of their resemblance to *Solenites* he may well have been right. Later authors endorsed Heer's view that *Leptostrobus* is allied to *Voltzia*, and as far as I know the first expression of another view was my opinion (1935) that it belonged to *Czekanowskia. Czekanowskia* and *Leptostrobus* are associated on many of Heer's figured blocks, but he selected some other fossils as fructifications.

Association

Association between fossils proves only one thing: that they were more or less associated during life, occurring at the same time and in the same district. It is chiefly when such association is repeated that it becomes impressive.

A second general point is that leaves are nearly always commoner than reproductive organs, except in floras sorted by floating great distances in water, and none of the present floras is of that type. It follows that where several unassigned specimens of a reproductive organ are found, its foliage is most probably present in some abundance.

Leptostrobus laxiflora and *L. crassipes* are both frequent in Heer's flora and they are associated with two species of *Czekanowskia* in two districts, namely, Ust-Balei and Kajamündung. The association is fairly close (they sometimes occur on the same blocks), but Heer's text does not show how general and perfect the association may be.

Kryshtofovich (1933) figured a specimen of *Leptostrobus laxiflora* and one of *Czekanowskia* apparently from Heer's original locality. This confirms the association but does not add to the evidence.

I prefer not to rely at all on the various Russian Jurassic fossils described by Schmalhausen (1879) as *C. rigida*. These include leaf fragments which could be of that or other nature, and fructifications which could be *Leptostrobus* capsules (though others look different).

In the basal Liassic rocks of east Greenland *L. longus* occurs as a rare fossil in three localities. These are Cape Stewart *Todites* Bed; Storgaad R. Plant Bed and Vandekløft *Czekanowskia* Bed. The three localities have rather different plant associations, but in all three *C. hartzi* is abundant. *C. hartzi* is, on the other hand, a common fossil in Greenland and is known from fifteen localities.

A specimen of *Leptostrobus*, cf. *laxiflora* or cf. *longus*, has been recorded from Japan by Oishi & Takahasi (1936) and Oishi (1940), from the Liasso-Rhaetic rocks of 'Loc. 16 Yamanoi'. *Czekanowskia* sp. is recorded by Oishi (1940) from 'Loc. 1 Yamanoi', the two being of the same age but a short distance apart; there is no mention of *Czekanowskia* in 'Loc. 16', the flora of which has not been fully listed. I cannot therefore base any argument on this record, though it may be hoped that this matter will be investigated.

Turutanova-Ketova (1930) figured an isolated capsule determined as *Leptostrobus laxiflora* Heer in a flora including *Czekanowskia* from the Kirghiz (south-west Siberia). Its age is Jurassic, a good deal younger than the Rhaetic. The figure gives no detail.

While collecting at Cloughton, by far the best of all the Yorkshire localities for *Solenites*, I looked for and was pleased to find *Leptostrobus* associated with it. This locality is a classic one and has yielded quite a large flora, but as it happens no other species which closely resembles *L. cancer* in cuticle. The actual blocks with *L. cancer* have the following species in or near the layers where *L. cancer* occurs:

Solenites vimineus, overwhelmingly abundant.
Ptilophyllum pecten with its flowers (*Williamsonia*) and its bracts (*Cycadolepis nitens*).
Nilssonia tenuinervis (a cycad).
Coniopteris hymenophylloides (a fern).

The block of the Gristhorpe type of matrix in the Yorkshire Museum with *Leptostrobus cancer* is not properly localized, but I am sure it came from the Gristhorpe Bed, since it has the character of that bed at its most typical and is a type of shale known from nowhere else. The associated species are among the commonest at Gristhorpe, namely:

Nilssoniopteris vittata (Brongniart).
Nilssonia compta (Phillips).
Coniopteris hymenophylloides (Brongniart).
Solenites vimineus (Phillips).

Summary of the evidence of association

Leptostrobus is associated with *Czekanowskia* (or *Solenites*) in eight localities as follows:*

East Greenland, basal Lias	3 localities
Yorkshire, Lower Oolite	2 localities
Eastern Siberia, Upper Jurassic	2 localities
South-western Siberia, Jurassic	1 locality

On the other hand, while *Leptostrobus* is a rare fossil, *Czekanowskia* is abundant and has been found in many places where *Leptostrobus* is unknown. I have compared the floras of these eight localities, and they have no other genus of leaf in common apart from *Czekanowskia* (including *Solenites*).

Agreement in structure

(1) *Basal scale leaves.* Heer is the only author who has seen and figured the basal scale leaves of *Leptostrobus*. These scales look very like those at the base of the leafy shoots of *Czekanowskia rigida* and *C. setacea*. On the other hand, they do not resemble the leaves of any other associated plant.

(2) *Cuticle.* The studies of various authors culminating in the systematic work of Florin has shown that in the gymnosperms, at any rate, there is a considerable degree of uniformity in epidermal structure over many of the exposed parts of a species. The stomata in particular tend to conform to a standard type, and it is possible to use them as well as other epidermal features to relate isolated organs of different categories to one another.

Only two species of *Leptostrobus*, *L. longus* and *L. cancer* have been studied microscopically, and their structure is almost exactly the same.

The cuticles of the leaves and of the fructifications agree in the general character of their epidermal cells and in the details of their stomata. They differ, however, in the dimensions of the cells and in the frequency and arrangement of the stomata.

(*a*) *For* Leptostrobus longus *and* Czekanowskia hartzi

The agreement between the cuticles of the leaf and cone axis is close but it is rather less close between the leaf and capsule wall. The leaf has an epidermis with rows of elongated cells with straight, conspicuous lateral walls and a smooth, non-papillate surface. The axis of the cone shares these characters. The leaf has stomata which are monocyclic (encircling cells are rarely present). The thinly cutinized guard cells have a longitudinal aperture and are sunken at the bottom of an elongated rectangular pit. The subsidiary cell group is rather irregular but always elongated; it commonly has terminal subsidiary cells and one or two lateral ones on each side. The subsidiary cells are nearly as large as ordinary epidermal cells, but their surface is usually a little thicker. Their surface has no papilla, but a small rim of cuticle projects from the lateral subsidiary cells over the sides of the stomatal pit.

The stomata of the cone axis are exactly as in the above description, and the dimensions of all their parts is the same as in the leaf. They differ, however, in frequency and arrangement. In the leaf they are often placed in obscure longitudinal files and they are quite frequent (up to 50 per mm.^{2}). On the cone axis they are very sparse and scattered. The

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* *Leptostrobus cancer* and *Solenites vimineus* have been found together in a third locality in 1951, namely at Cloughton 30 ft. above the Iron Scar.

capsule wall has larger and much broader epidermal cells, which in some specimens give a suggestion of a median papilla. The stomata are larger and relatively broader than on the leaf, but are mostly of the same elongated shape; a few are rounded. They are more frequent than on the axis, but again they are scattered, not forming definite files.

So far as is known trichomes are entirely absent from leaf and cone.

(*b*) *For* Solenites vimineus *and* Leptostrobus cancer

Some variation was noticed among the many leaves studied, and the agreement is closest between the cone axis and those leaves with more elongated cells. Nearly everything said in the description of *Czekanowskia hartzi* applies equally in the description of *Solenites vimineus*, except that the cell walls though straight often show minute jagged thickenings, and the cells are often not much elongated. The subsidiary cell group is often just as in *Czekanowskia hartzi*, but it may be relatively broader, and there is a greater tendency for encircling cells to occur. Trichomes are nearly absent, but a very few do occur, and these are confined to the angle of the dichotomy. These trichomes are simple, more or less conical prolongations of ordinary cells. The cone axis shows elongated straight-walled cells with minute jagged thickenings. A very few trichomes occur, and these are simple cylindrical or conical prolongations of ordinary cells. The stomata are very few but seem just like the more elongated ones on the leaves; other stomata on the axis seem ill-developed. The fruit wall again shows broader cells than either its own axis or the leaf. The stomata are rather varied. Some specimens show stomata with longitudinally orientated guard cells, rectangular pit and an elongated group of subsidiary cells much as on the leaf, but the whole size and especially the width is greater. Other capsules have a large proportion of their stomata of varied orientation and surrounded by a rounded group of subsidiary cells. Encircling cells are frequently present, and in some capsules constantly present.

I believe that the features of agreement and of disagreement between the cuticles of leaf, cone axis and capsule wall are of just the kind to be expected between different organs of one species.

Czekanowskia hartzi is the only Greenland leaf associated with *Leptostrobus longus* with a cuticle closely resembling *Leptostrobus*. The next nearest would be *Sphenobaiera spectabilis* (which is found with it in all three localities), but its strongly papillose epidermal and subsidiary cells are very different indeed. Other Greenland localities of about the same age do, however, provide a few species with some similarity, namely, *Czekanowskia nathorsti* and *Stenopteris dinosaurensis*. Neither, however, is associated with it anywhere and neither is as close to it in structure as *Czekanowskia hartzi*.

Solenites vimineus is the only leaf associated with the Yorkshire *Leptostrobus cancer* which resembles it at all in structure. The blocks bearing *L. cancer* provided the flora mentioned above on p. 500. Other Yorkshire localities, however, provide a few species which approach *L. cancer* to some extent; these are *Czekanowskia microphylla*, an undescribed *Czekanowskia* of the Upper Deltaic, and *Stenopteris nana*. Various Ginkgo and undescribed conifer leaves approach it more remotely.

The structural agreement between *Czekanowskia* (or *Solenites*) and *Leptostrobus* is thus very marked and shared by no associated species. This structural evidence, taken together with the evidence of repeated association summarized on pp. 500, 501, affords circumstantial evidence for supposing they all belong to one group of plants. Each additional piece of such supporting evidence adds materially to the probability of the hypothesis. I was already convinced in 1935 that there were strong reasons for referring *Leptostrobus* to *Czekanowskia*. Since then they have been found associated in two additional Yorkshire localities, an additional Siberian one (the Kirghiz), an additional Greenland one, and perhaps in an additional one in Japan. The agreement in structure now extends to a second species.

6. Classification of *Leptostrobus* and *Czekanowskia*

Czekanowskia, taken without any fructification, but with the very similar leaves *Solenites* and *Hartzia*, would be easy to classify in the Ginkgoales. *Leptostrobus*, on the other hand, is like the fruit of no known plant, recent or fossil, and is in my opinion unclassifiable in any existing family.

There has been no dispute about the position of *Czekanowskia* for many years, and Florin (1936) discussed its position exhaustively and decided that he regarded it as an extreme member of the series of fossil leaves assigned to the Ginkgoales. I myself have expressed such an opinion.

Czekanowskia agrees with *Ginkgo* in the dichotomous plan of its leaf; it has the same general type of cuticle, though this type is by no means exclusive of the Ginkgoales. The same may be said of the internal anatomy of the leaf. The strongest arguments in favour of its Ginkgoalean alliance is that there is a great series of fossil leaves linking it with *Ginkgo*, and there is little in this series to suggest a division, quite the reverse indeed. The reader is referred to Florin (1936*a*, *b*) for a full statement of the points of agreement.

Differences are:

(1) The lamina is divided into filiform segments.

(2) The lamina as a whole is wedge-shaped (with no petiole), while in *Ginkgo* it is distinctly petiolate.

(3) The leaves are borne on a short caducous shoot of strictly limited growth. In *Ginkgo* they are borne on long shoots or on short shoots of unlimited growth. In this respect *Czekanowskia* is like *Pinus* while *Ginkgo* is like *Larix* or *Cedrus*.

(4) There are differences in the arrangement of the stomata and in the shape of the subsidiary cell group.

(5) Though the leaf of *Czekanowskia* has secretory cavities, their contents is not preserved in macerated leaves. In fossil leaves closely resembling *Ginkgo* the resin masses are remarkably resistant to maceration.

(6) The leaf base of *Czekanowskia* has but one vascular bundle, while *Ginkgo* has two.

The first five differences seem to me to be of the kind which might all occur in a natural phylum and be rightly used for distinguishing the genera. The last difference may be more important.

Florin, who discovered this difference in leaf trace number, at first rather discounted its importance. He argued that the Ginkgoales primitively had a single bundle which is seen in these fossil genera, but that in the recent and advanced *Ginkgo* the first dichotomy extended backwards to the stem. Later, however (Florin 1949, p. 103), he revised his view, as a result of the discovery that in *Ginkgo* the two leaf-trace bundles have a separate origin and are not merely the result of early division. He therefore emphasized the possible phyletic importance of this difference between certain of the fossils and *Ginkgo*.

Other leaves besides *Czekanowskia* were shown to have a single basal bundle; these include *Windwardia crookalli* and *Arctobaiera flettii*, both of which share with it the caducous short shoot and absence of a petiole. The fructification of neither is known. Another species with a single basal bundle is *Sphenobaiera horniana*, but here the material is fragmentary and there is nothing to show how the leaves were borne.

The position for the leaf alone is thus: *Czekanowskia* is either a member of the Ginkgoales or it is a member of another order with leaves almost exactly like those of the Ginkgoales. If it belongs to another order, this order is certainly unknown, and there is no other order with claims to include *Czekanowskia*.

The nearest genus, outside the 'Ginkgoales', seems to me *Stenopteris*. Several species of *Stenopteris* have leaves with linear, forking segments, and the cuticle is very like that of *Czekanowskia* indeed. In *Stenopteris nitida* the midrib of the leaf may dichotomize, and in a series of southern hemisphere leaves placed in *Stenopteris* dichotomy is normal, but there is still a difference in the way the leaf branches. In its central region *Stenopteris* branches pinnately, very commonly with opposite pinnae, a kind of branching foreign to *Czekanowskia*. (One species, *C. microphylla*, shows a slight approach to pinnate branching.) Another difference is that the leaves in *Stenopteris* are preserved separately, presumably having been borne on shoots of indeterminate growth, while in *Czekanowskia* they are on caducous short shoots. Nothing is known of the rest of the plant in the typical northern species of *Stenopteris*, but the southern hemisphere ones appear to have borne reproductive organs of the *Umkomaasia* and *Pteruchus* groups (Thomas 1933).

No one has suggested that *Czekanowskia* is related to *Stenopteris*, and it is not suggested here, but until both are better understood it is a possibility which should not be excluded from thought.

The opinion has already been expressed that *Leptostrobus* is unique and unclassifiable. Certain recent and fossil plants do, however, show points of approach or agreement, and these will now be reviewed.

Several Bennettitales produce two-valved capsules rather like the capsule of *L. cancer*, but less like that of the other species. However, instead of a row of seeds, it has been repeatedly proved that there is a row of elongated pollen sacs. The way the capsules are borne also is very different, and this comparison will not be pursued.

The fossil now named *Harrisia marsiliodes* (Harris) Lundblad, 1950 (=*Hydropterangium marsilioides* Harris non Halle) has several striking points of resemblance to *Leptostrobus*, but I believe it has fundamental differences.

The main 'axis' gives off branches on all sides (as in a cone), but these branch repeatedly and end in robust two-valved capsules looking very like those of *L. cancer*. In view of my mistakes in dealing with *L. longus* I reinvestigated some of the slides of *Harrisia*, and I found that one of the *Harrisia* capsules (no. 1551) which is slightly immature proves beyond dispute that it is a pollen-bearing organ. Every one of the pollen sacs is intact, and each contains many hundreds of the characteristic medium-sized winged pollen grains. As a pollen-bearing organ it is separated completely from *Leptostrobus*.

It is possible to compare one valve of *Leptostrobus* with any of the following:

a single *Caytonia* fruit,
a *Cycas* megasporophyll,
a *Cupressus* cone scale,
a several-seeded cupule of a Lower Carboniferous Pteridosperm,
a two-seeded cupule of one of the Triassic Pteridosperms (*Umkomaasia*).

In each case it would seem to me possible to start with the embryonic initial of the organ in question (imaginary in the fossils) and to suppose it proceeding by a perverted development to give a *Leptostrobus* valve. However, when the two-valved capsule is considered, *Cupressus* and *Cycas* are to be left out, and the series of stages leading to the others become more elaborate, particularly if one valve is really over the other. None of these comparisons will be followed in detail because I can see no gain from it, but of course new facts might make it worth while.

A comparison with a bicarpellary ovary of an angiosperm is possible, but the differences are great, particularly in pollination, which in *Leptostrobus* is Gymnospermous. The approach to an Angiosperm capsule in this Gymnosperm genus does, however, remain interesting as an early organ with much of the biological function of a closed ovary.

Leptostrobus is remote from the female fructifications of the Ginkgoales. In this group we know: (1) *Ginkgo biloba*; (2) a few closely similar fossils associated with fossil *Ginkgo* leaves; (3) certain moderately similar but more branched fructifications associated with *Baiera gracilis* (see Black 1929); (4) similar fructifications associated with *Baiera muensteriana* (see Florin 1949, p. 95); and finally (5) *Trichopitys heteromorpha* Sap. recently described and discussed by Florin (1949). This remarkable plant bears axillary female 'trusses' which seem to be very like the more richly branched type of female organ found in *Gingko biloba.* Microscopic details are lacking, but the appearance of the 'seeds' strongly suggests that they are true seeds and not little seed-bearing capsules like those of *Leptostrobus.*

My imagination can only bridge the gap between any of these Ginkgoales and *Leptostrobus* by going right back to a Psilophytalean type of organization of telomes and phyllomes. This is another way of saying they seem unrelated.

Leptostrobus (with *Czekanowskia*) has in fact the same sort of relation to the Ginkgoales as *Taxus* has to the conifers. *Taxus* and its immediate allies agree perfectly with the conifers in their vegetative organs, but the organization of the female organs is so different as to make any relationship too obscure to be profitable to follow at the present time.

Leptostrobus requires a new major group to accommodate it, but for reasons given below this group is not yet proposed.

(1) It seems very likely that a fresh study of really good material, such as that originally described by Heer, would greatly enrich and perhaps materially alter any characterization at present possible. In particular, it is desirable to know more about the organization of the seed. It is unfortunate also that male organs are lacking.

(2) Such a new group must include the leaves *Czekanowskia*, *Solenites* and probably *Hartzia*, but there is at present nothing to indicate a boundary between the new group and the remaining Ginkgoales. For instance, the position of *Arctobaiera* and *Sphenobaiera* would be doubtful and this would be a real disadvantage.

Further work may bring to light the fruits of such genera and settle this matter. The existing classification of 'Ginkgoalean' leaves including *Czekanowskia* proposed by Florin is of considerable practical value, and though the present work indicates that it includes botanically unrelated plants, this does not necessarily lessen its usefulness.

When framed, the characters of the new group will include those of the foliage genus *Czekanowskia* and the cone *Leptostrobus*, but I hope they will include wider knowledge than simply the sum of the diagnoses of those two genera.

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Description of plates 18 and 19

Plate 18

Figure 5. Partly cleared valve showing fragments of two seeds, V28571. (Magn. × 10.)

Figure 6. Part of the specimen shown in figure 5 showing the chalazal ends of the seeds in each of which a black megaspore is surrounded by a border of integument tissue. (Magn. × 20.)

Figure 7. Partly cleared valve showing fragments of four seeds, V28572. (Magn. × 10.)

Figure 8. Part of the specimen in figure 7 showing the chalazal ends of seeds connected by elongated cells with the valve margins. (Magn. × 20.)

Figure 9. Fragment of megaspore membrane showing cell-like folds (unusually marked in this fragment) and conspicuous granules, V28573. (Magn. × 100.)

Figure 10. Nearly intact megaspore membrane of unusually small size dissected out from a macerated capsule, V 28574. (Magn. × 40.)

Figure 11. Capsule as exposed by cleavage showing a little matrix between the two valves (photo under paraffin), V28561. (Magn. × 10.)

Figure 12. Capsule isolated by HF and cleared by maceration. The valves are somewhat displaced, V28575. (Magn. × 10.)

Figure 13. Fragment of the fibrous inner membrane of a capsule (which also gave the megaspore in figure 10). The curvature of the upper part suggests a seed integument, V28574. (Magn. × 100.)

Figure 14. Capsule as exposed by rock cleavage; part of the upper valve is broken away and exposes some of the matrix inside. The matrix itself is missing above where the inner surface of the lower valve is exposed. *Solenites* leaves occur beside the capsule. Photo under paraffin, V28561. (Magn. × 10.)

Figure 15. Capsule as exposed by rock cleavage, the lower part of the upper valve has broken away exposing enclosed rock matrix. Photo under paraffin, V28561. (Magn. × 10.)

Figure 16. Isolated valve freed by balsam transfer, seen by transmitted light. Note the vein-like appearance of the ribs. (The same specimen is seen under different lighting in figure 2F.) Type specimen, V28568. (Magn. × 10.)

Figures 17, 18. Two capsules exposed by rock cleavage with different parts of the upper valve broken away exposing the matrix filling the interior. Photos under paraffin, V28561. (Magn. × 10.)

Figure 19. Part of the slab which is believed to have provided the originals of Phillips's figure, pl. 7, fig. 25. Four capsules in various stages of damage are seen, as well as several leaves of *Solenites vimineus*. Photo under paraffin. (Magn. × 2.) York Museum.

All the figures are untouched photographs taken by Mr L. C. Willis.

Plate 19

Figures 21, 28 represent the Greenland specimen of *Leptostrobus longus* previously called *Microcheiris enigma*. Figure 27 represents *Solenites vimineus*; the rest are all *Leptostrobus cancer*.

Figure 20. Cuticle of valve wall. The stomata in figures 3A to C are from this specimen, V28569. (Magn. × 150.)

Figure 21. *Leptostrobus longus*, a new photograph of the specimen shown in Harris (1935, pl. 8, fig. 6). Note the five lobes under each of which is a megaspore, under each of which is a small mass of pollen. The 'fibrous membrane' is broken away at the base of the capsule. Greenland slide 2881. (Magn. × 12.)

Figure 22. Wall of isolated valve in the region of a rib showing fibres and rounded hypodermal cells, V 28576. (Magn. × 100.)

Figure 23. Wall of isolated valve (seen also in figure 16) showing some of the thick-walled cells. Drawing on a photo, V 28568. (Magn. × 100.)

Figure 24. Small mass of pollen grains dissected out of the capsule shown in figure 26, V 28578. (Magn. × 100.)

Figure 25. Fragment of associated axis showing broken-off appendage, V 28579. (Magn. × 10.)

Figure 26. Unopened capsule containing dark matter which is chiefly seed megaspores. The small masses of pollen are labelled *P*. Specimen subsequently dissected. V 28577. (Magn. × 12.)

Figure 27. *Solenites vimineus* cuticle, thinner side, V 28591. (Magn. × 150.)

Figure 28. Central part of the specimen shown in figure 21 more magnified. The lower ends of the three middle megaspores are seen together with their pollen masses and there are many stray pollen grains adhering to the fibrous membrane. Four small round cavities are visible in the megaspores (possible archegonial neck openings) and are labelled *A*. Greenland Slide 2881. (Magn. × 60.) The figure in Harris (1935, pl. 8, fig. 5) represents the left megaspore and also shows an archegonium like cavity.

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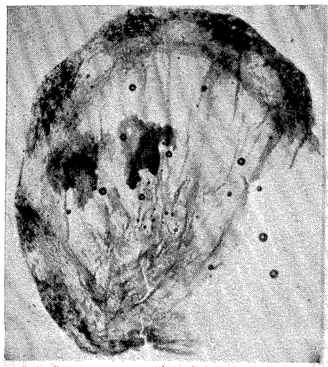
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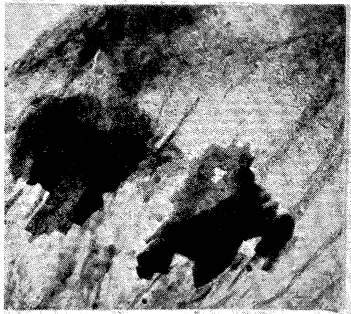
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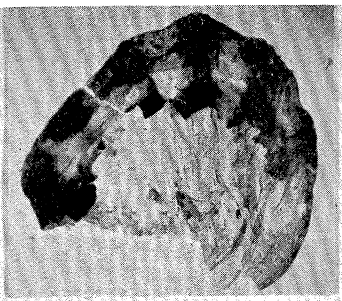
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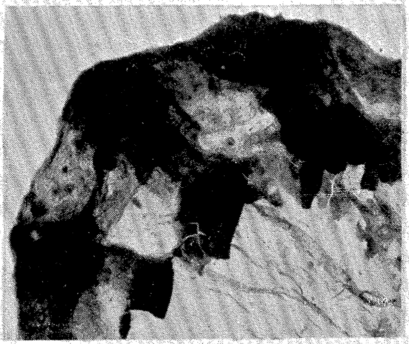
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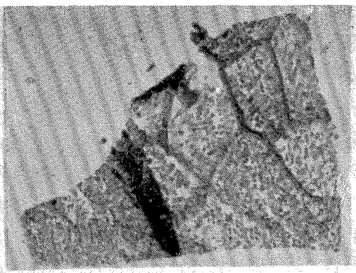
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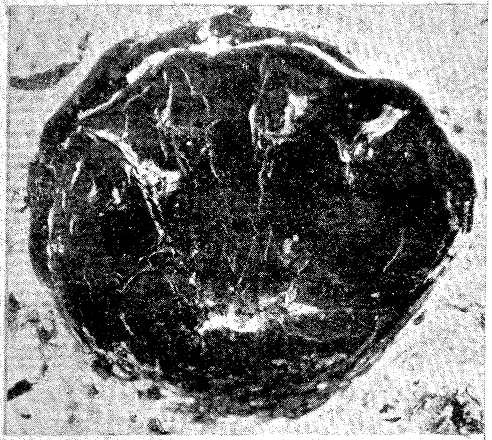
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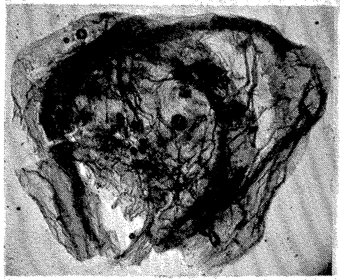
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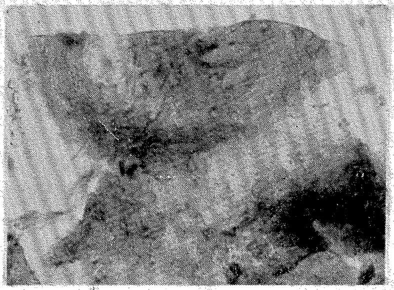
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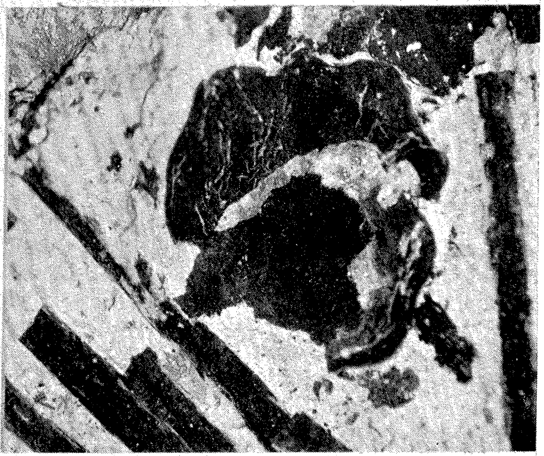
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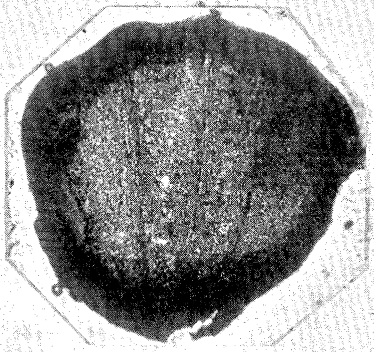
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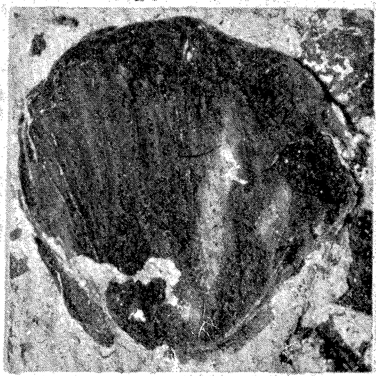
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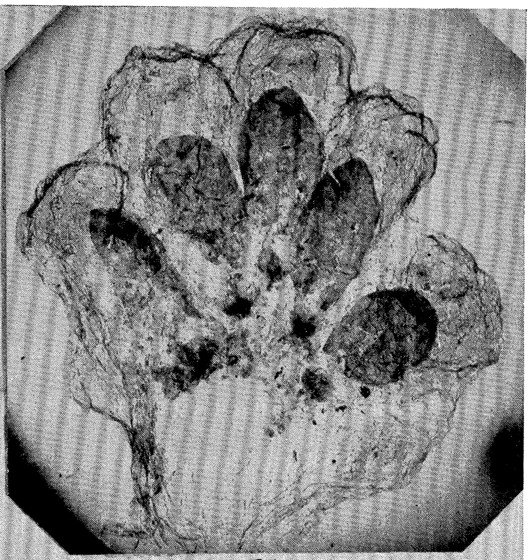

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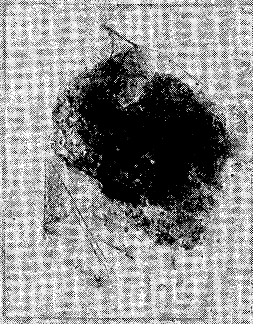

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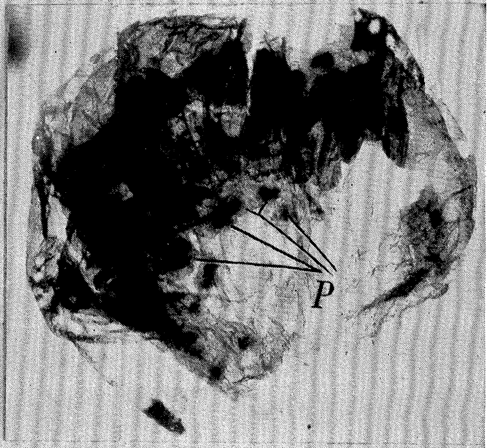

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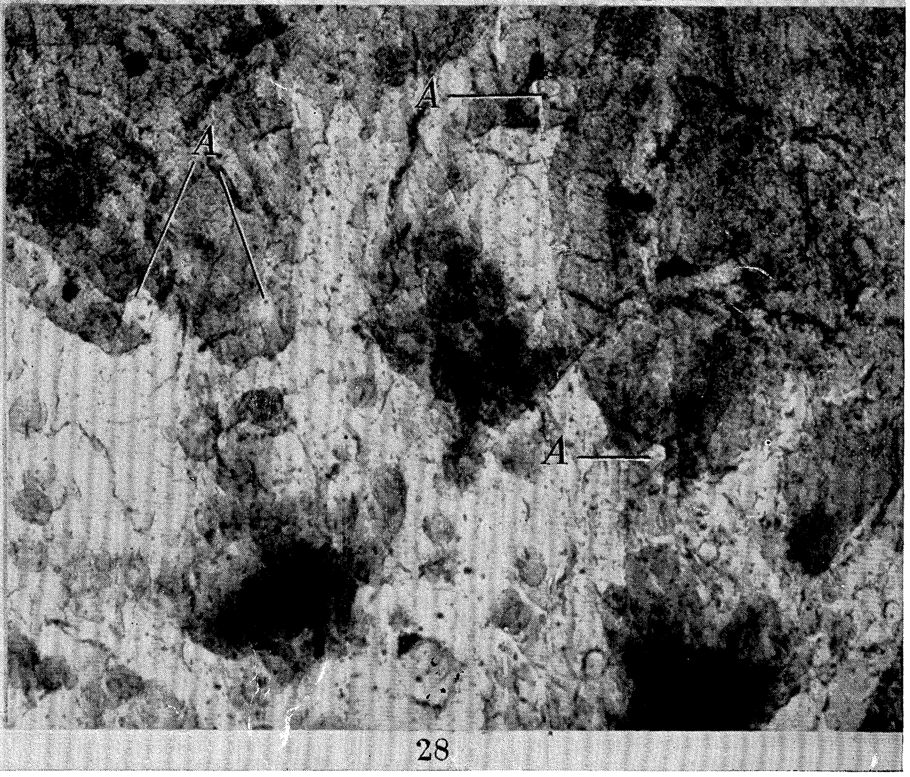

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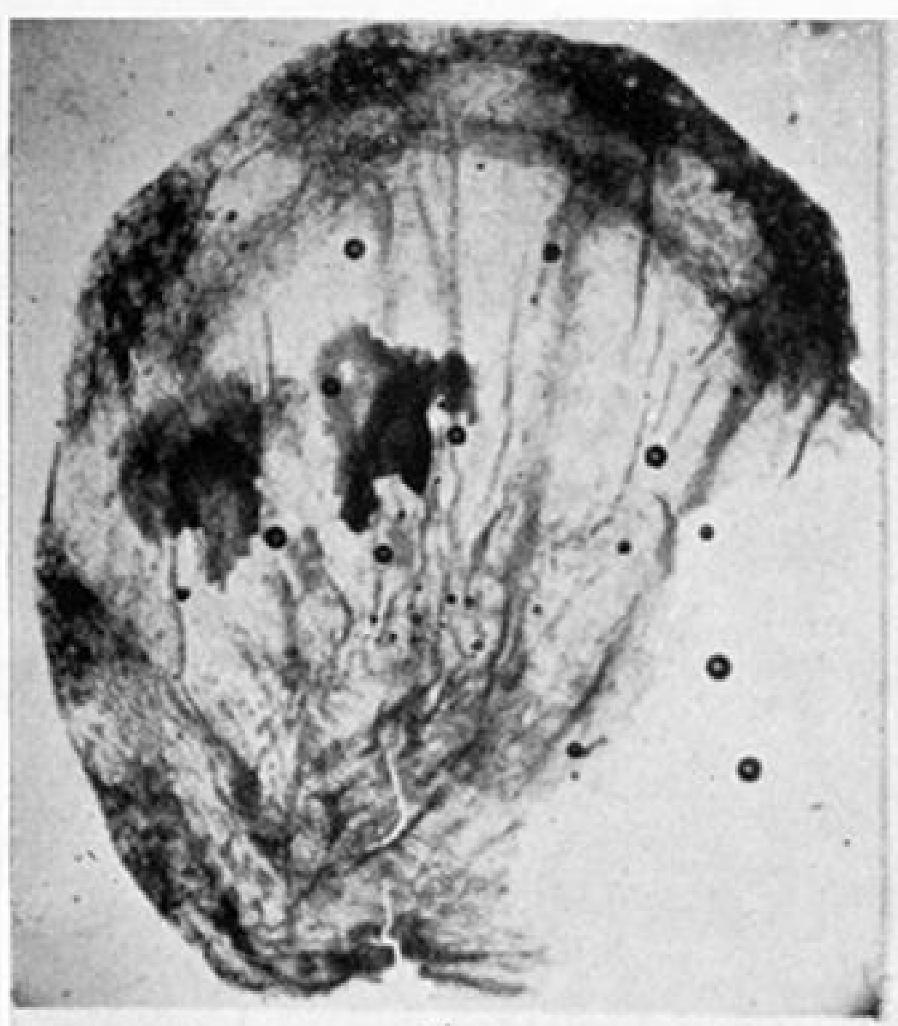

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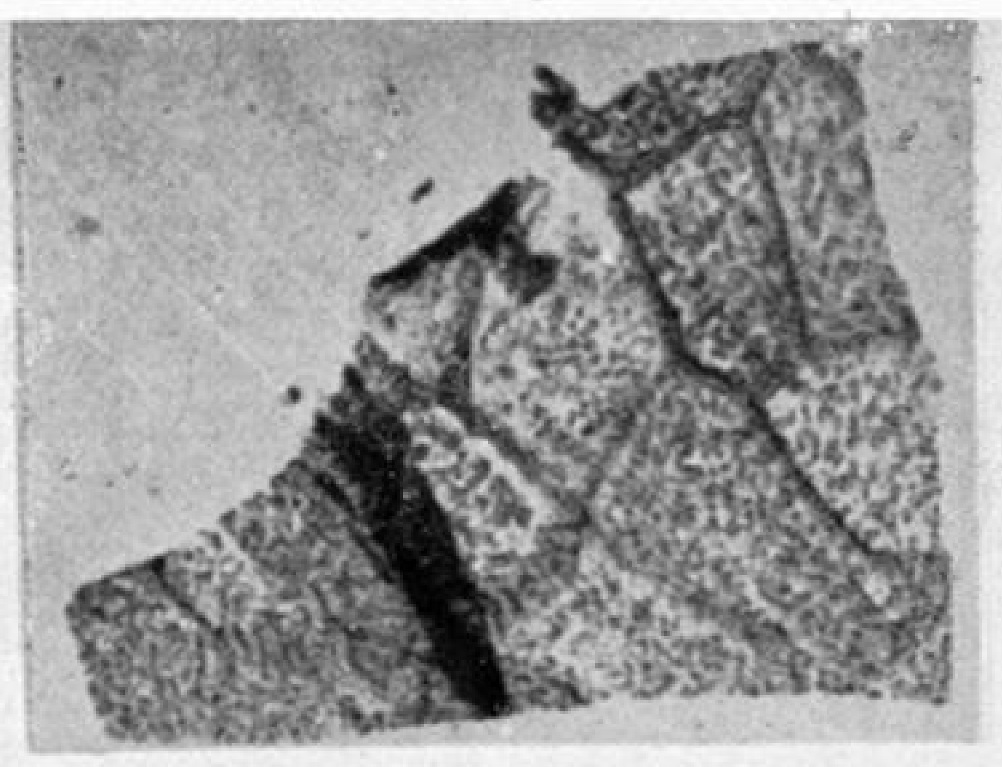

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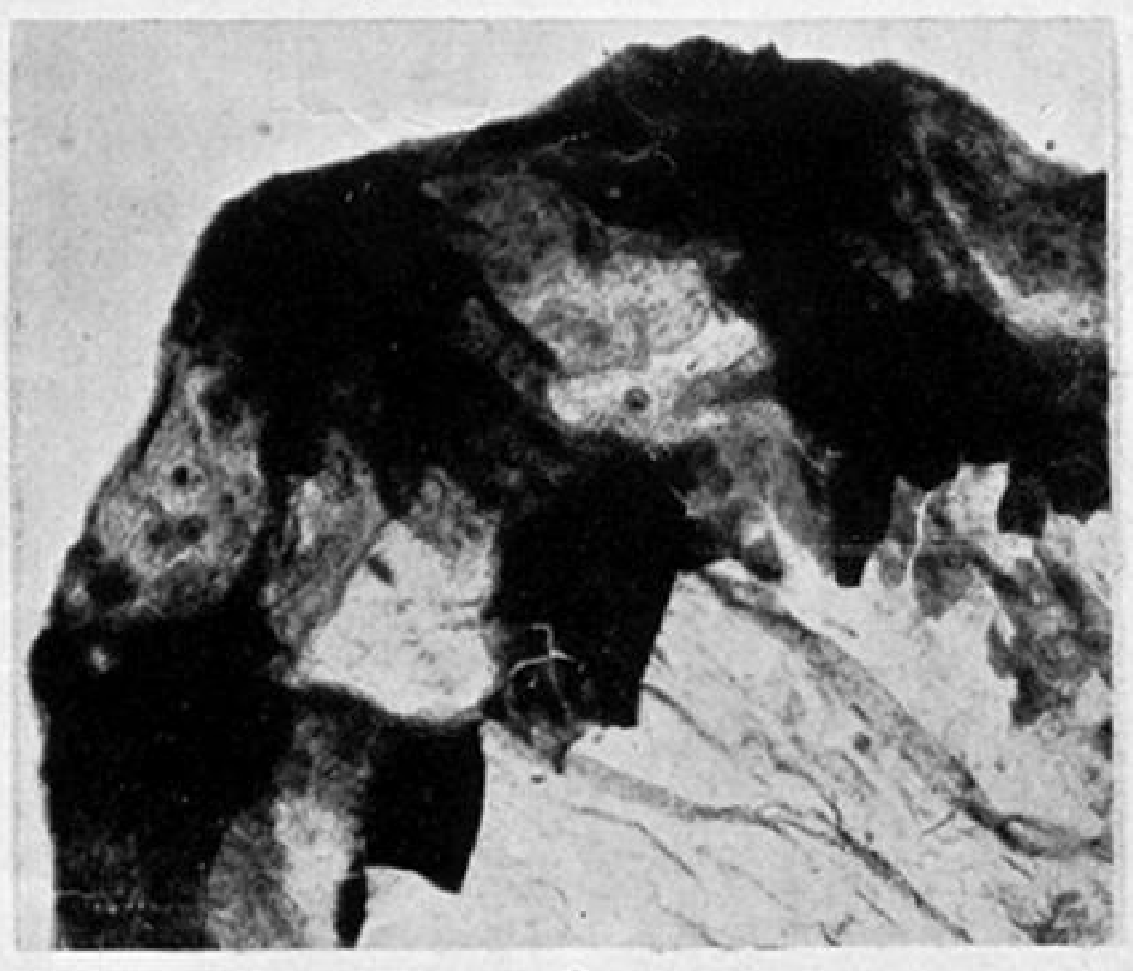

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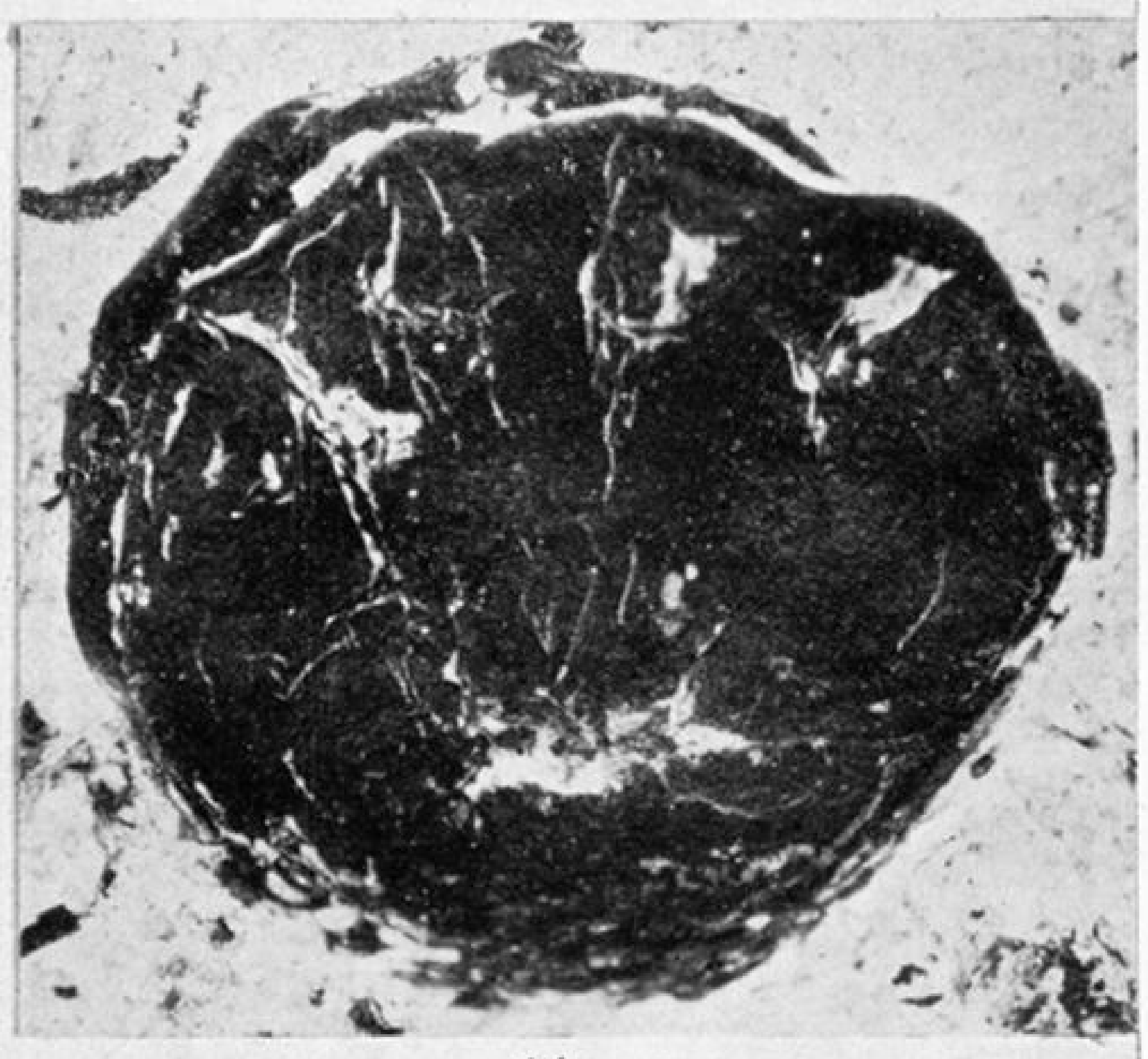

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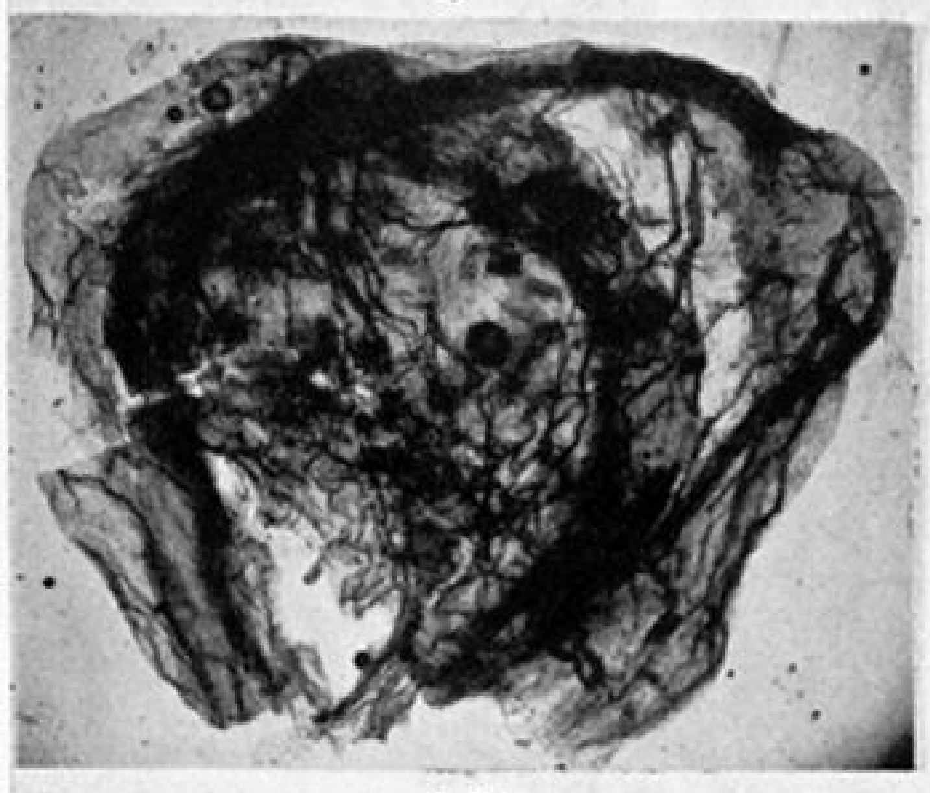

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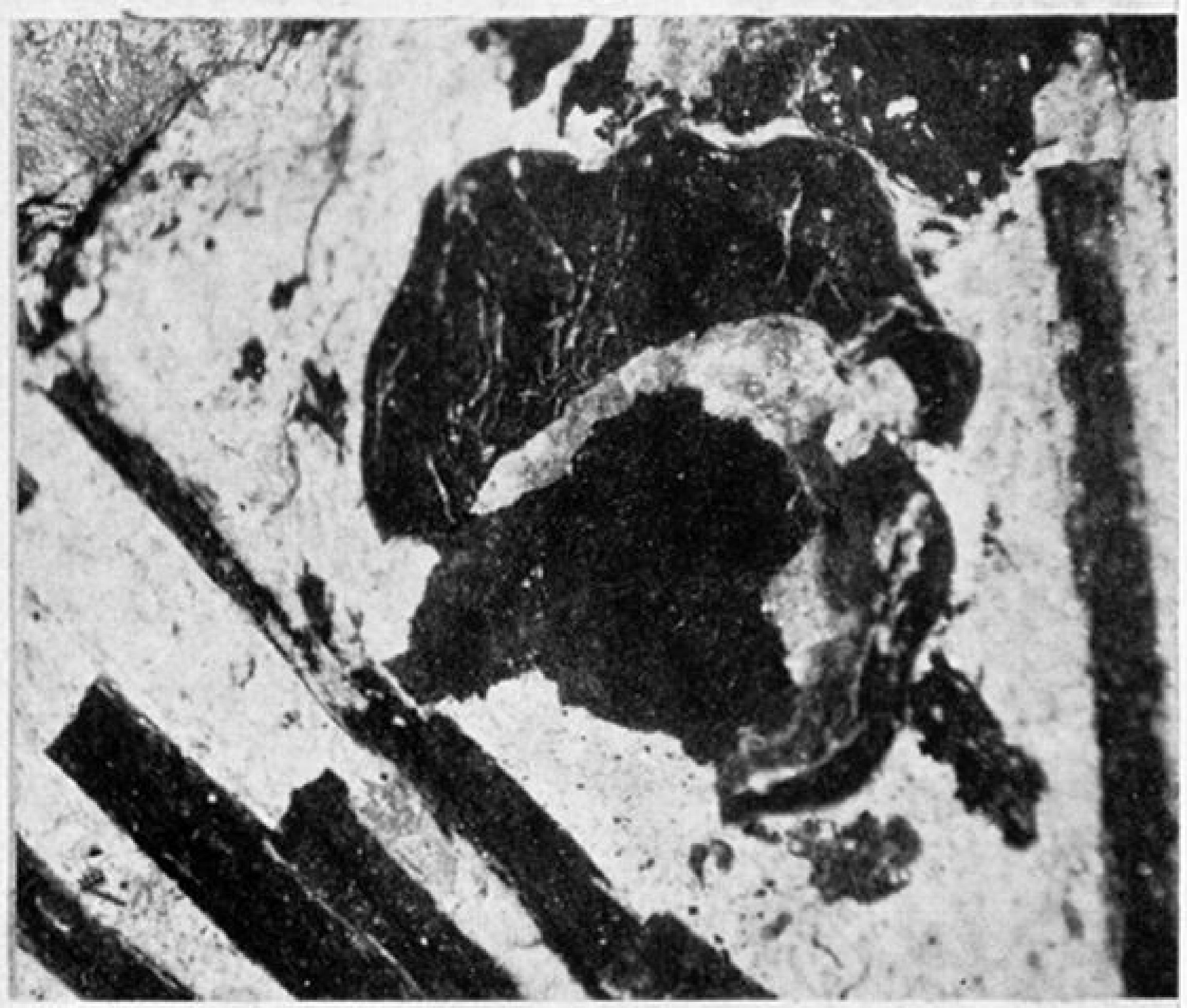

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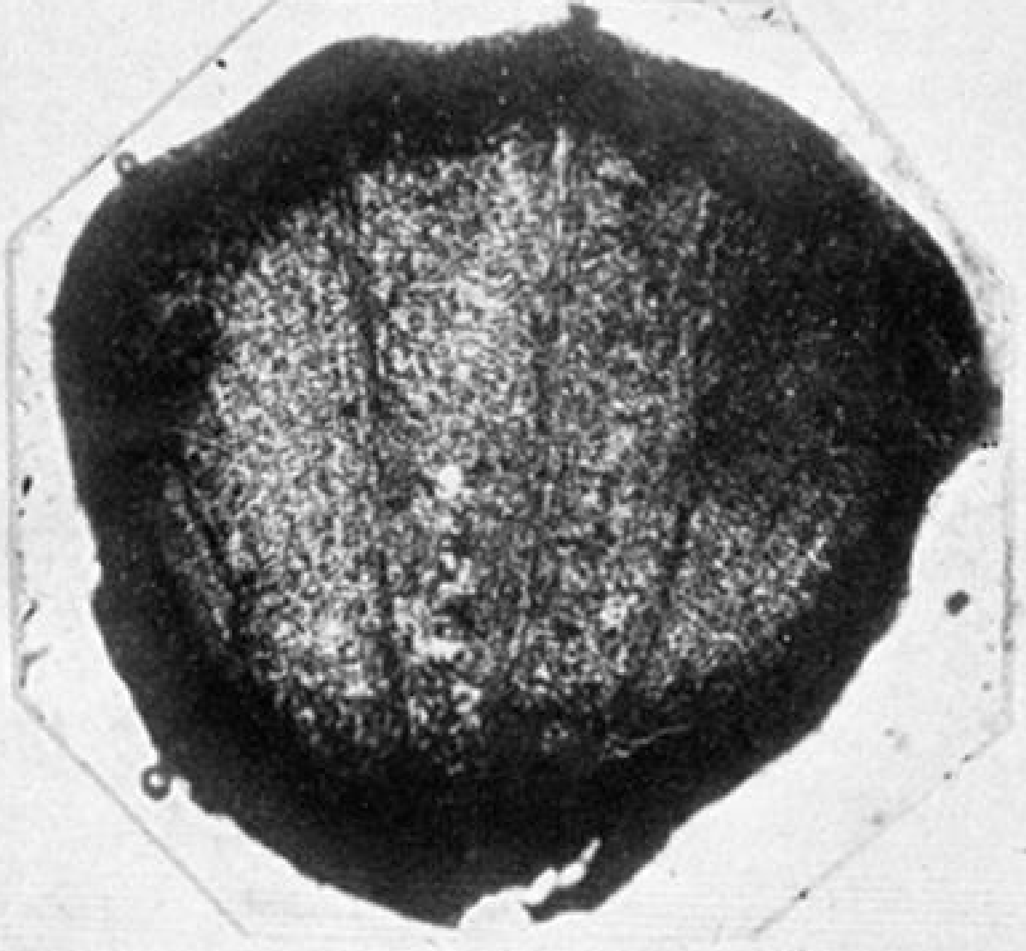

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Plate 18

Figure 5. Partly cleared valve showing fragments of two seeds, V 28571. (Magn. × 10.)

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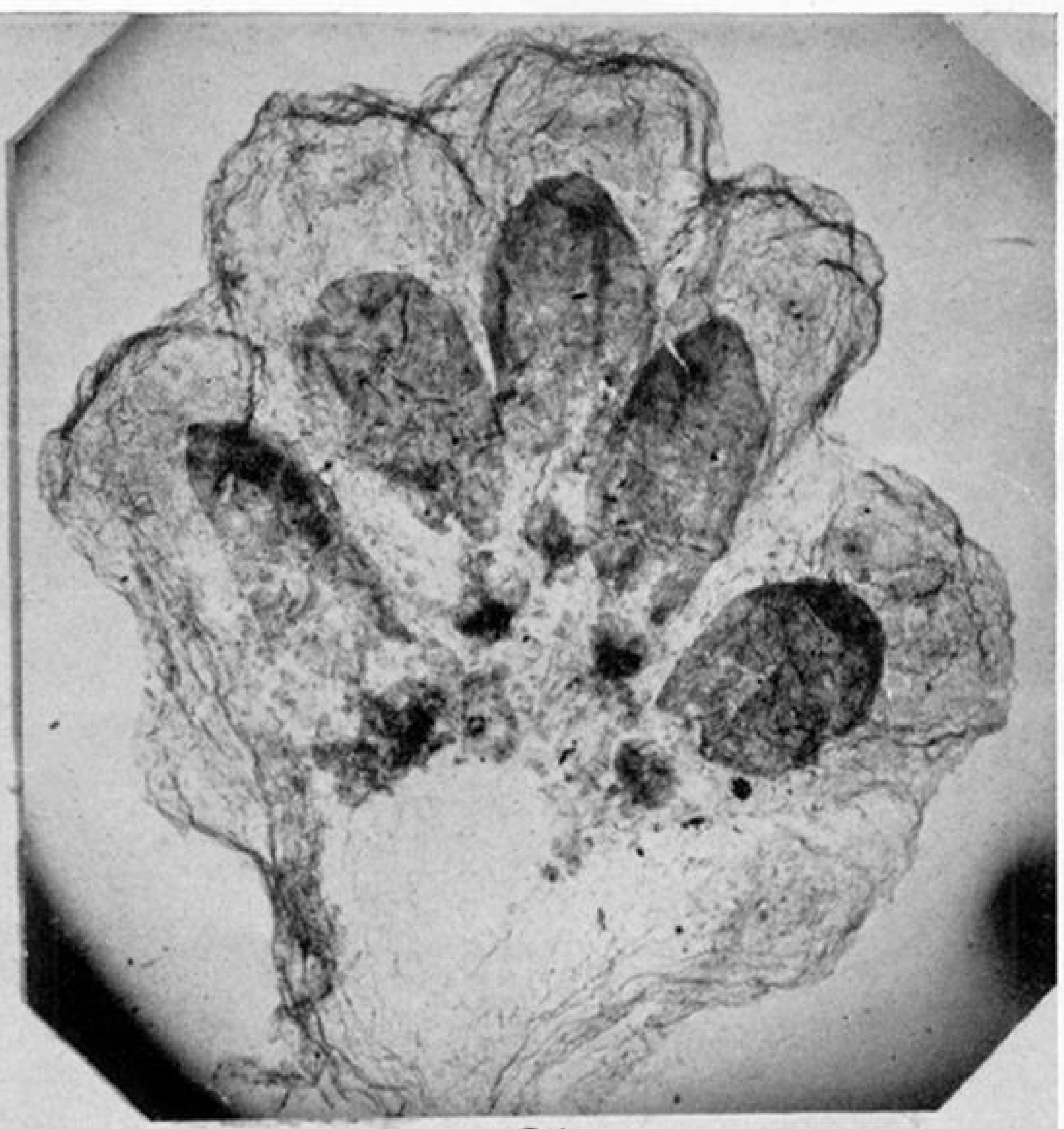
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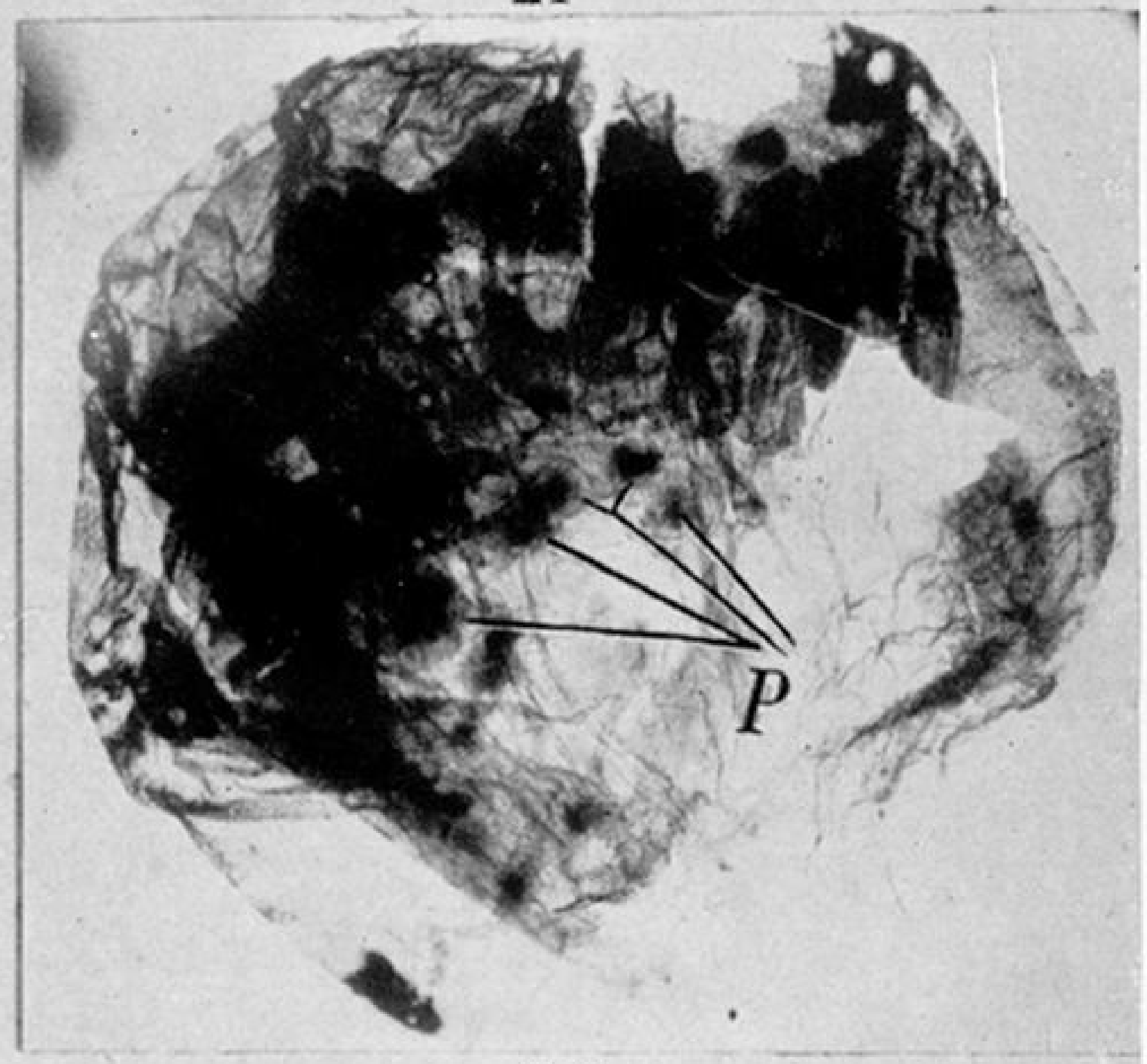

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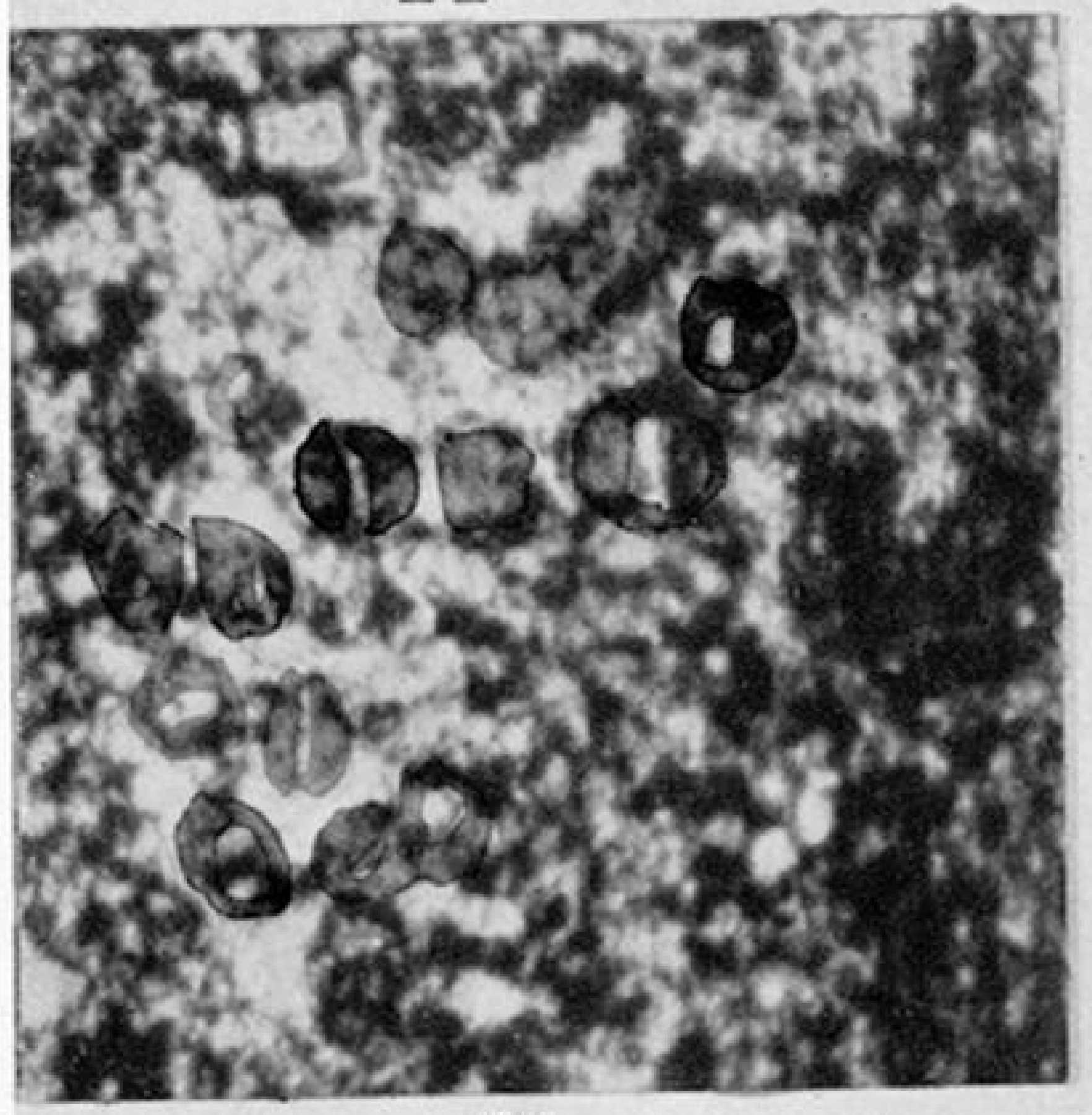
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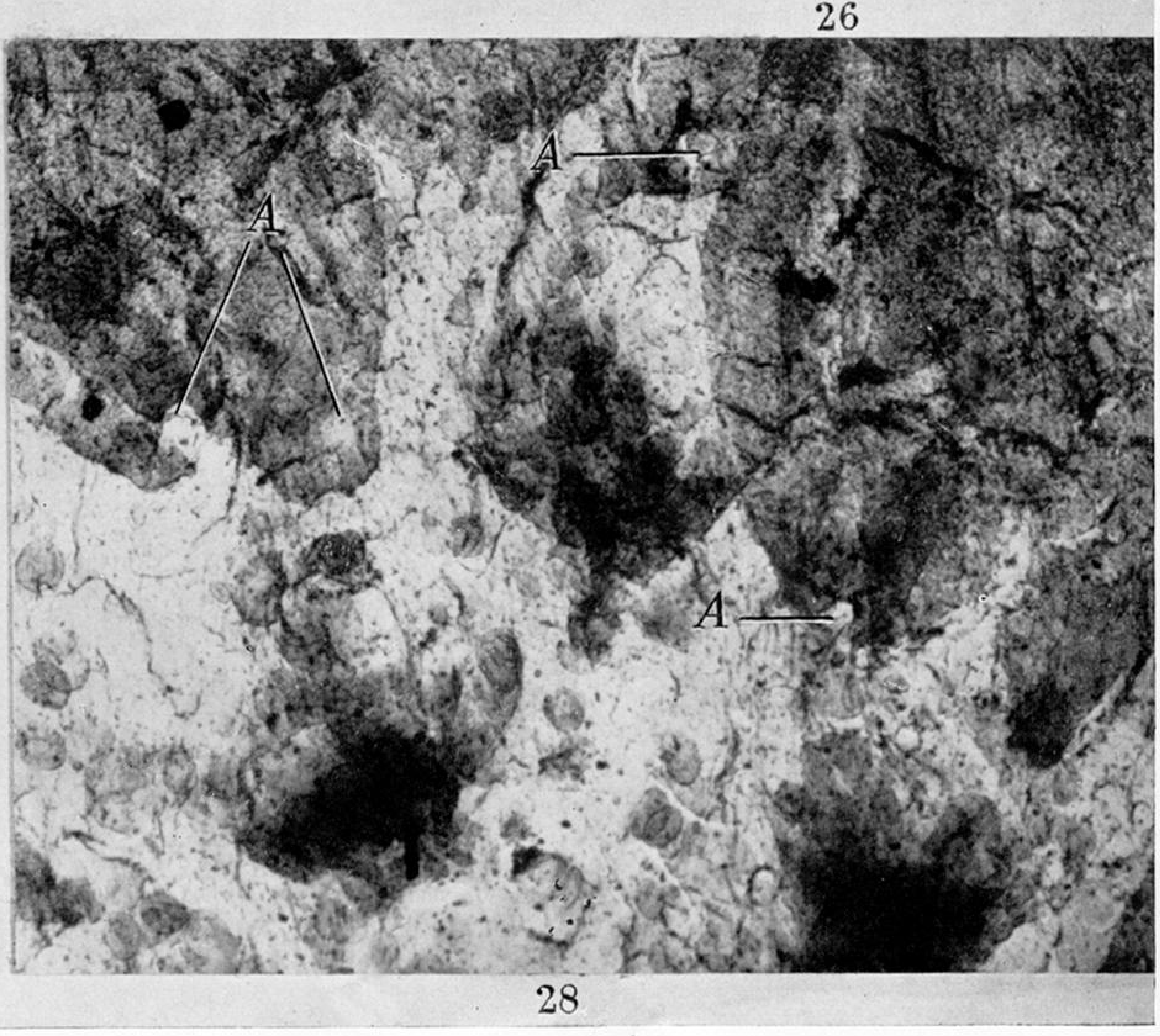

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