FURTHER OBSERVATIONS ON THE LOWER DEVONIAN PLANT, *GOSSLINGIA BRECONENSIS* HEARD

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[Plates 34 to 38]

CONTENTS

The first description of this plant was published by Heard (1927). The present writer has collected more material from the type locality and has used a comparatively new technique on the petrified axes present. This involved sawing the axes into thin sections, grinding these smooth with carborundum powder and then polishing them in chromic oxide powder. These permanent preparations have yielded more precise data on the anatomy of the axes. The spores are described for the first time. A reconstruction of the aerial parts of the plant is given. The results have been incorporated into an emended diagnosis of the genus and a lectotype has been designated. The taxonomic position of *Gosslingia* is discussed in relation to a new classification of the psilophytes proposed by Banks. One of the most interesting features in *Gosslingia* is the axillary tubercle, a small protuberance occurring below each dichotomy. A survey of other Devonian plants bearing this structure is given and its morphological nature is discussed in the light of evidence produced here and in other recent work.

1. Introduction

The last decade has seen a great revival of interest in Devonian palaeobotany. Although some of this has centred around the discovery and description of new species, much has originated from the re-investigation of species already known, but inadequately studied. Indeed, new information

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on the anatomy and morphology of several Devonian plants has necessitated changes in their long accepted reconstructions and also in their taxonomic positions. Such investigations prompted the present author to look again at the plant material found in the sedimentary deposits of the Lower Old Red Sandstone of South Wales. The extensive Senni Bed flora of Breconshire and Monmouthshire was last reviewed by Croft & Lang (1942). The subject of this paper, *Gosslingia breconensis*, although included in their work, was originally described by Heard (1925, 1927).

In his preliminary report in 1925, Heard had called the plant *Psilophyton*, but he renamed it *Gosslingia* when he presented an account of its anatomy and morphology in 1927. He investigated the anatomy of a pyritized axis by etching the polished end with concentrated nitric acid. He then photographed the surface, ground it smooth and repeated the procedure. As this technique destroys the specimens, only a photographic record of the anatomy remains. Unfortunately, apart from those used in the paper, Heard's photographs have been lost.

Heard's findings are conveniently summarized in his generic diagnosis:

> '*Gosslingia* Heard, gen.nov.
>
> Plant rootless and leafless, with stomata and hairs. Gregarious, erect stems cylindrical, dichotomously branched, arising from dichotomously branched rhizomes with rhizoids; branches exhibiting equal dichotomy, subordinate to a stouter sympodial main axis showing unequal dichotomy; stems circinately coiled in apical regions. Stem consisting of a large strand of tracheids with spiral and reticulate thickening, surrounded by protoxylem and phloem; outer cortex of aerial stem consisting of four layers of thick-walled cells; oval sporangia borne on special branches, which emerge from immediately below the bifurcation of the stems on the sympodial main axis.'

Although not apparent in the diagnosis, Heard also described small protuberances on the surfaces of the axes and stated that the projections (later called axillary tubercles by Høeg 1942) commonly found immediately below the branching points were the bases of the fertile branches.

One of his illustrations (plate XIV, figure 3) shows the exarch protoxylem particularly clearly.

Gosslingia was later described from Llanover Quarry by Croft & Lang (1942). They examined compression fossils only, but their results agreed essentially with those of Heard, except that they found no fertile branch in the position of the axillary tubercle. Instead, they described lateral sporangia on both main and lateral branches and thought that the axillary tubercle represented the base of a small slender branch, although they had no evidence to support this. They reported that axillary tubercles occurred on one side only of the branching system. They also suggested that the sporangium on dehiscence separated into two valves.

The present investigation has yielded further information on the axillary tubercle, the branching system, the anatomy of the axes, the distribution of sporangia and the spores of *Gosslingia*.

2. LOCALITIES

Most of the material studied in this investigation was collected by the author at the Brecon Beacons Quarry. Some specimens from this locality and from Llanover were borrowed from the Croft Collection in the Department of Palaeontology, British Museum (Natural History). The collection made by Heard, now housed in the Department of Geology, National Museum of Wales, was also examined.

(2.1) *Brecon Beacons Quarry*, an abandoned roadside quarry on the A470 between Brecon and Merthyr, approximately 7½ miles south of Brecon, SO. 972208. The majority and best preserved of the plant remains were found in a very fine-grained, blue-grey, fissile sandstone, containing films of mudstone. This plant bed was about 15 cm thick and outcropped on the front part of a 3 m wide, prominent ledge, situated on the west face of the quarry. This ledge was nearly 7 m above road level. By now, the plant layer has been almost completely removed.

(2.2) *Llanover Quarry*, a disused quarry in a small beech wood on a scarp above Llanover, south of Abergavenny, SO. 298079.

Both quarries occur in the Senni Beds, i.e. in the lower part of the Breconian Stage of the Lower Old Red Sandstone of South Wales (≡Siegenian-Emsian). The stratigraphic occurrence of *Gosslingia* is considered more fully in §7.

3. MATERIALS AND METHODS

The plants from the Brecon Beacons Quarry are preserved either as heavily carbonized compressions or as pyrites petrifactions, but only vegetative axes are found pyritized. At Llanover, heavy weathering has resulted in the almost complete disappearance of the carbon, and the fossils are usually represented by orange stains on the rock. In addition, the iron sulphide in the petrifactions has been oxidized to the yellow-brown iron oxide, limonite. Most of the anatomy recorded below was taken from the fossils collected at the Brecon Beacons Quarry.

Bulk maceration of the rock in 40% hydrofluoric acid released very small fragments of cuticle, which were cleared with Schulze's solution. As it was impossible to determine the exact location of such fragments on the axes or indeed to know whether they were actually derived from the plant under investigation this was unsatisfactory. These difficulties were partially overcome by pouring a solution of cellulose nitrate in amyl acetate over the fossil and leaving it to dry overnight. The resulting transparent film was pulled off and mounted. Occasionally pieces of cuticle bearing the outlines of cells were recovered on the film pull, but where carbon was present, this could not be cleared with Schulze's solution. Film pulls of sporangia were particularly informative as they occasionally showed spores *in situ*. By dissolving the film in amyl acetate, it was sometimes possible to recover the spores.

Petrified axes were treated in the way outlined by Edwards (1969). To obtain permanent preparations, instead of etching with nitric acid the cut axes were first ground smooth using carborundum and then polished with chromium oxide powder.

4. DESCRIPTION OF PLANTS

(*a*) *Morphology*

Axes

No complete plants were found, although large slabs of rock completely traversed by plant axes were collected. One of these is illustrated in figure 2, plate 34. This specimen shows the typical parallel alinement of axes in the matrix, with those of similar diameter lying close together. The widest axes, assumed to be from the basal aerial regions of the plant, measure up to 4 mm in diameter, while the smallest ones, presumably from the apical parts, are 0.5 mm wide. This assumption that there is a decrease in axis diameter from the basal to the apical regions of the plant is borne out by the decrease in diameter noted along individual axes. Taking into account the longest one found which measured 15.0 cm and comparing its dimensions with those of both fertile and sterile axes, it is deduced that the height of the plant is at least 50.0 cm.

Branching is predominantly by unequal dichotomy. This gives the impression of a monopodial branching system with a wide main axis and smaller alternate lateral rows (figure 1, plate 34). The latter divide in the same way, but the narrow penultimate axes fork equally (figure 12, plate 35). Dichotomous branching is rare in the wider axes. The distance between lateral branches near the base of the main axis is up to 2.0 cm, but branching occurs more frequently towards the apex.

Circinately coiled axis tips are sometimes seen in the matrix but seldom found attached to the axes (figure 19, plate 35). The rare occurrence of such tips may be explained by the fact that some of the plants examined are probably mature fertile ones, in which the tips have already uncoiled. Figure 14, plate 35, shows an axis bearing sporangia which ends in a small hook. Occasionally, however, a sporangium is seen on the inside of a coiled tip. Small hooks have also been seen terminating sterile axes (figure 12, plate 35).

Below equal and unequal dichotomies on both sterile and fertile axes are structures, which have been named axillary tubercles (Heard 1927; Høeg 1942) (figures 3 and 4, plate 34). The term is misleading in that the tubercle is not axillary but is found a short distance below a branching point and in pseudomonopodial branching may be slightly displaced toward the side of the lateral branch. Axillary tubercles are always found in pyritized specimens, but are sometimes absent in compressions, probably due to preservation failure. In compression fossils, tubercles are represented by either oval swellings or depressions (figure 3, plate 34) while in petrifactions there are definite projections (figure 4, plate 34). When transverse sections were cut from petrified axes, the axillary tubercle was cut longitudinally, and measured on average 0.94 mm long by 0.69 mm wide. The longest one found is 1.32 mm long. Axillary tubercles project at right angles from the plane of the main branching system and occur on one side of the axis only.

Specimens bearing the letter V. are housed in the British Museum (Natural History), the remainder, 69.64.G, are housed at the National Museum of Wales, Cardiff.

Description of plate 34

Gosslingia breconensis, figures 1–11

Figure 1. Sterile region of plant, showing typical pseudomonopodial branching. × 1. (V. 26574.)

Figure 2. Parallel axes on rock. Petrified regions are indicated by arrows. × 0.65. (69.64.G1.)

Figure 3. Axillary tubercle below branching point on compression fossil. × 10. (69.64.G2.)

Figure 4. Pyritized axis with axillary tubercle below branching point. × 3.5. (69.64.G3.)

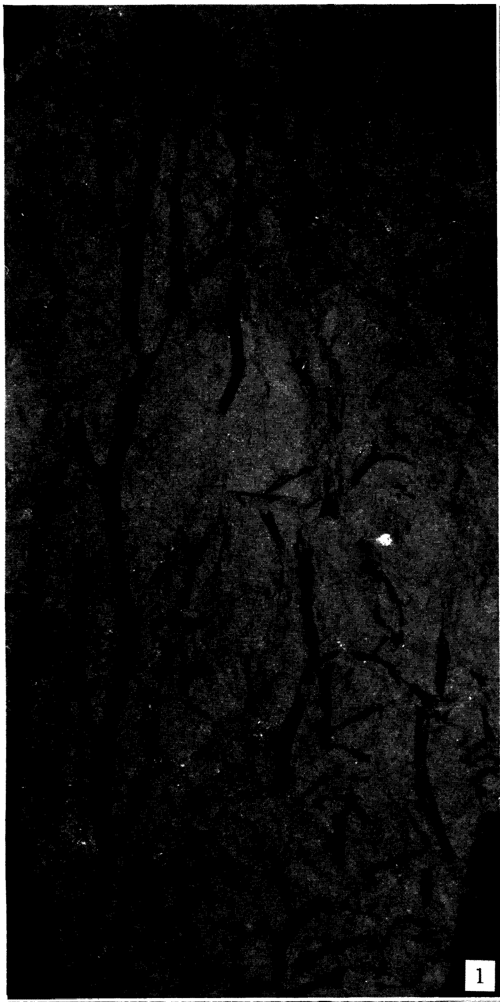
Figure 5. Pyritized axis with outlines of cells on the surface. × 8. (69.64.G4.)

Figure 6. Electron scanning microscope photograph of part of axis illustrated in figure 5. × 58. (By courtesy of the Cambridge Instrument Company.)

Figure 7. Petrified axis with small protuberances. × 4.5. (69.64.G5.)

Figures 8, 9. Transverse section (TS) through outermost region of axis, figured in 7, showing outer cortical tissue and protuberances. × 120. (69.64.G5–2 and 69.64.G5–7 respectively.)

Figures 10, 11. Film pull from sterile axis showing possibly epidermal cells. × 165. (69.64.G15.)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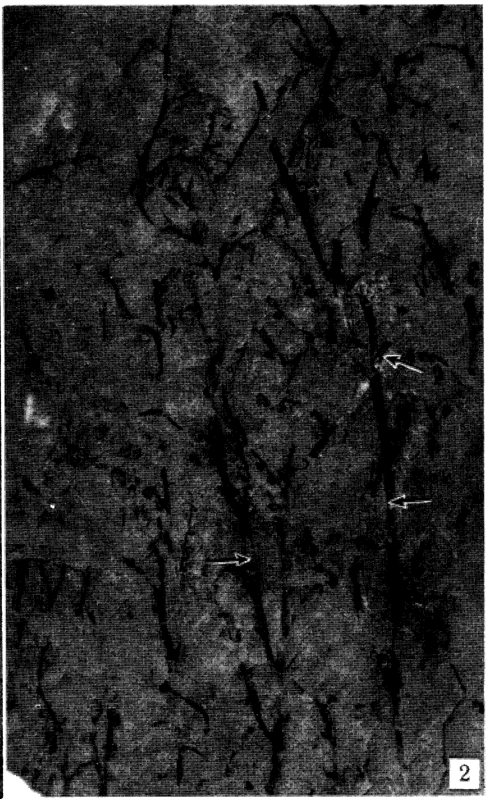
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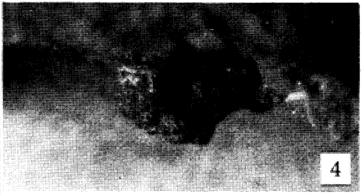
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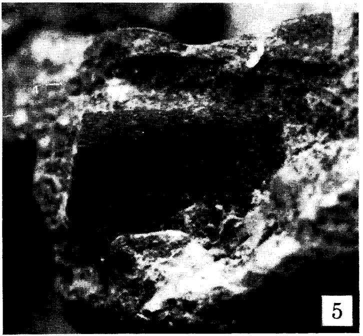
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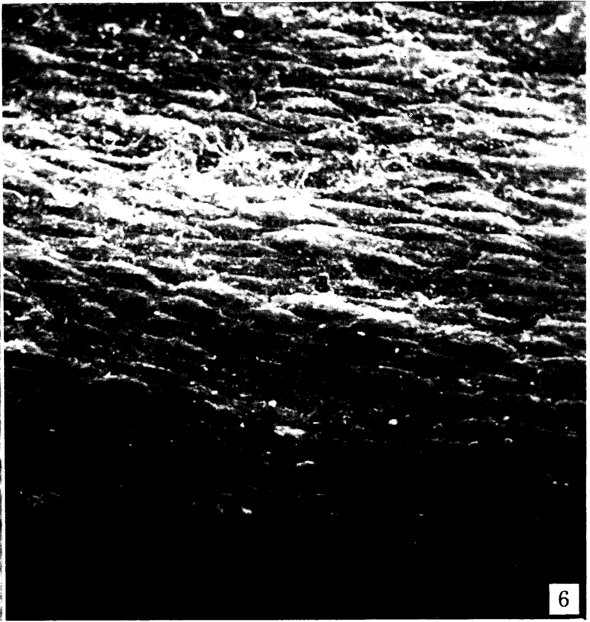
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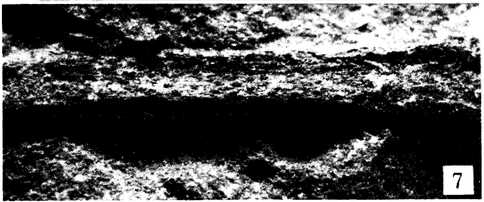
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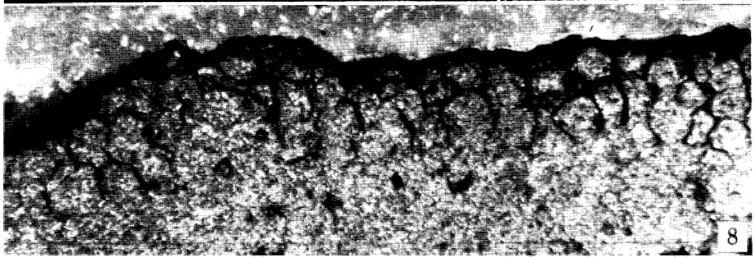
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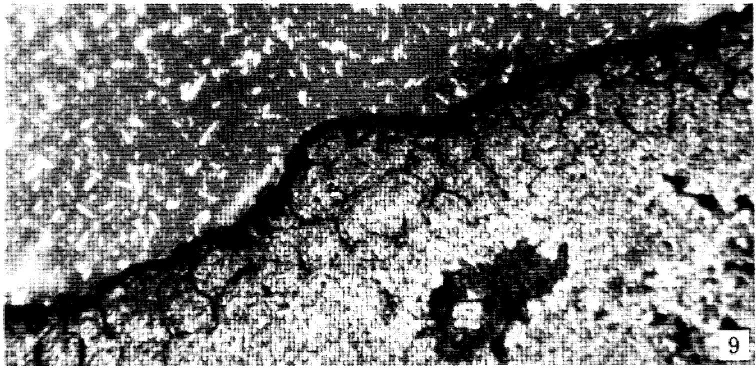
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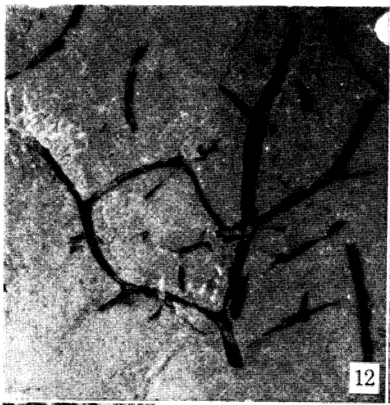
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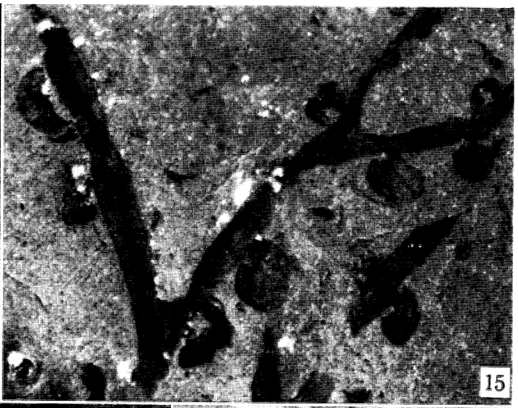
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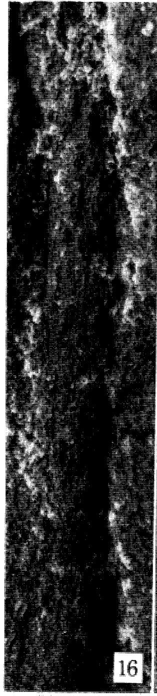
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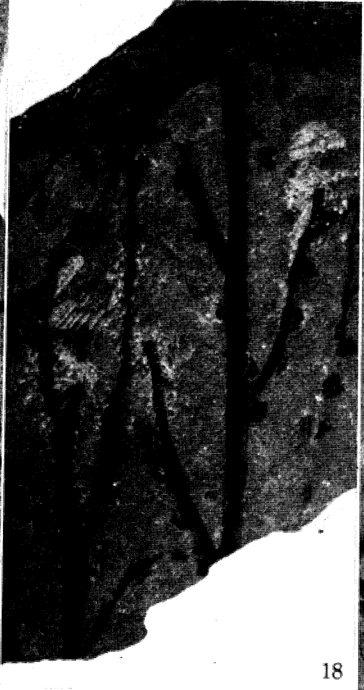
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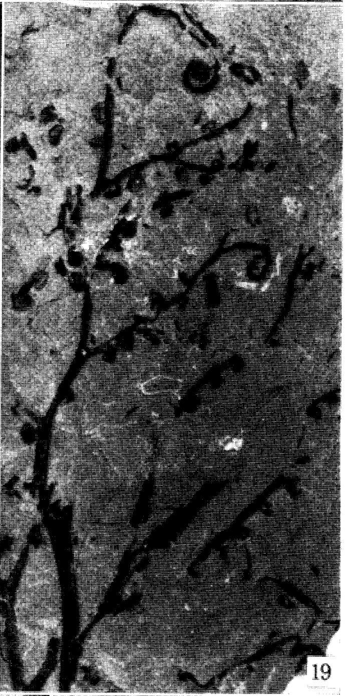
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Sporangia

It has already been indicated that Heard thought that the axillary tubercle was the base of a sporangial branch. The results presented here, in agreement with those of Croft & Lang, show that the sporangia are not borne on special fertile branches but are scattered on the sides of both the main and lateral branches. The distribution of sporangia in relation to the whole plant however is still unknown. It is probable that there is a definite fertile region, where sporangia are very numerous, at least 20.0 cm from the base of the plant. Whether this is followed by a sterile region distally could not be determined conclusively, but certain very narrow axes, ending in hooks and bearing no sporangia, have been found. In one specimen there are sporangia on the lower parts of the branching system, but none within 2.0 cm of the tip (figure 13, plate 35). It is, of course, possible that some axes are sterile throughout.

Sporangia occur on both sides of the main axes, but on the outer side only of the lateral branches. The most typical arrangement occurring at the base of the sporangial region, where branching is strictly pseudomonopodial, is as follows. A sporangium is found on one side of the main axis just below the base of the lateral branch (figure 18, plate 35). Up to five sporangia are borne on the lower surface of this branch. Associated with an almost equal dichotomy of the axis is a more atypical arrangement in which sporangia are in opposite pairs on the axis below the dichotomy and above it occur on the lower sides of both branches. An alternate arrangement of sporangia has also been seen. Sporangia on the wider axes tend to be further apart and are larger, while those on the ultimate branches are small. They vary in size from 2.5 to 1.7 mm high by 2.2 to 0.9 mm wide. The shape of the sporangium also varies. The majority are oval to reniform (figures 15, 21, 23 and 25, plate 35) and have short stalks. The latter are on average 0.5 mm long and 0.4 mm wide. Exceptionally long stalks are sometimes seen (figure 22, plate 35). Some sporangia, particularly those nearer the distal parts of the plant, are globose and it is probable that these are immature. Certainly they are often more completely preserved than the larger reniform ones. In some specimens there is a decrease in size and change in shape of the

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Description of plate 35

Gosslingia breconensis, figures 12–25

Figure 12. Sterile branching system, possibly from ultimate regions of plant. Small hook terminating branch is indicated by arrow. × 1.1. (69.64.G6.)

Figure 13. Axis with sterile region beyond sporangia. × 1.1. (69.64.G7.)

Figure 14. Fertile branch terminating in small hook. × 4. (V. 26487.)

Figure 15. Fertile branches. × 4. (V. 26573.)

Figure 16. Petrified axis with protuberances. × 4. (69.64.G8.)

Figure 17. Pseudomonopodially branching axes with occasional sporangia. Petrified region with surface protuberances, illustrated in figure 7, plate 34 is indicated by arrow. × 1.1. (69.64.G5.)

Figure 18. Fertile axes showing the typical arrangement of sporangia on wider axes. × 1.1. (69.64.G2.)

Figure 19. Fertile axes. Circinate tips are indicated by arrows. × 1.1. (V. 26575.)

Figure 20. Dichotomously branching fertile axes. Note the orientation of the sporangia. × 4. (69.64.G9.)

Figure 21. Fertile axis with almost globose sporangia. × 4.7. (V. 26577.)

Figure 22. Sporangium with long stalk and distinct border. × 7. (69.64.G10.)

Figure 23. Reniform sporangium. × 13. (69.64.G11.)

Figure 24. Dehiscence line on sporangium. × 7. (69.64.G12.)

Figure 25. Reniform sporangium. × 6. (DE1.31.)

sporangia along a single lateral branch. The outer convex margin of the sporangium appears to be more heavily carbonized than the rest of the wall, forming a distinct border to the organ. This is most clearly seen in film pulls (figure 48, plate 38). On dehiscence the sporangium splits into two equal parts comparable with the two halves of the cockle, *Cardium* (figure 24, plate 35).

The normal orientation of the sporangium with respect to the axis bearing it, is seen in figure 25, plate 35. The surface view of the whole of one valve is visible, but the other is completely obscured. In one specimen (figure 20, plate 35), although the sporangia on one branch of a dichotomy are borne in this way, those on the other are bent upwards through 90° and folded so that half of the abaxial valve only is visible. This latter arrangement is very similar to that seen in *Zosterophyllum llanoveranum*.

Examination of both the compression and petrifaction material at high magnifications using reflected light gives some cellular detail. In the majority of the pyritized specimens, the surface is not smooth, but has a striated appearance, produced by the outlines of elongate cells (figures 5 and 6, plate 34). Occasionally the outlines are equidimensional and not regularly alined. Since the epidermis is rarely seen in the polished sections made from these axes, it is possible that the elongate outlines represent the long cells of the outer cortex. However, the possession of more than one type of epidermal cell has been noted in other Lower Devonian plants, e.g. in *Zosterophyllum myretonianum* (Lele & Walton 1961), so it is possible that both types of surface pattern reflect the shape of epidermal cells. Any detail in the carbonized compression is usually either masked by carbon cleavage lines and cracks, or compression during preservation has completely obliterated any surface features. In some of these compression fossils, however, a line marking the position of the central vascular strand extends along the centre of the axis. Very occasionally, where the carbon layer is thin, particularly on the sporangia, its surface appears irregular and warty. I think that these marks are produced by irregularities in the underlying matrix and do not reflect any anatomical features of the plant. Heard, however, described protuberances, which terminated in hairs, on the axes. The present investigation has yielded some evidence in support of this. In addition to the surface markings already described, occasional protuberances are seen on some, but not all, of the petrified axes. They are never found on the compression fossils. At first it was thought that the few axes on which the protuberances occur belonged to another plant, but subsequent examination has shown that the protuberances are often highly localized so that other parts of the axis surface are smooth. In addition, their anatomy is identical with that in *Gosslingia*. It is unlikely that the protuberances are confined to the lower parts of the plant as they are absent from axes of similar or larger diameter. In addition, protuberances are found in the lower part of the fertile region. Unfortunately there are no petrified axes available from the more distal parts for further comparison. I also think it unlikely that lumps, originally present on the now smooth axes, have been sloughed off as the black carbon layer, often bearing the imprint of underlying cells, is continuous over the smooth surface and no patches of yellow pyrites are visible. Lastly, in petrified axes, the occurrence of protuberances seems to be independent of the degree of compression, which has occurred. (This is in contrast to the heavily carbonized fossils, where extreme compression has completely obliterated them.) The protuberances appear to be randomly scattered over the axis surface. In figure 7, plate 34, they are so numerous that they present an almost whorled or spiral arrangement. They are elongate, measuring on an average 244 μm long, 152 μm wide and 100 μm high. On another axis (figure 16, plate 35) the lumps occur in groups of 3 or 4 and were slightly larger. No hairs were seen.

A reconstruction of the plant, based on the above data, is given in figure 54.

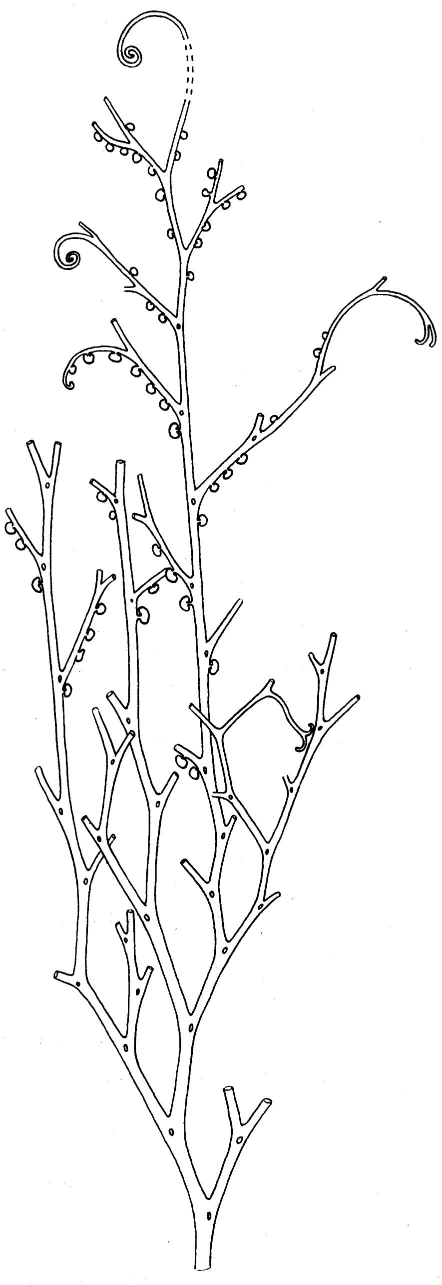


FIGURE 54. Reconstruction of the aerial parts of *Gosslingia breconensis*. ($\times \frac{3}{4}$.)

(*b*) *Anatomy*

Information on the anatomy of the axes was obtained, for the most part, from polished pyritized sections and occasionally from maceration material or film pulls.

The cuticle is represented in the pyritized material by a black line around the outside of the pyritized area (figure 28, plate 36). On the cleared, macerated fragments, it is a pale brown colour and occasionally outlines of epidermal cells are visible. These are of varying shape and size. Very often, longitudinal walls only are preserved but sometimes oblique end walls are present. The cells are several times longer than they are broad (figures 10 and 11, plate 34). Occasionally, angular isodiametric cells are also found. The epidermis is rarely preserved in pyritized material. Series 1–45 is an exception. Here again the great variation in the size of the cells can be seen (figures 26 and 27, plate 36).

At intervals, two adjacent cells of the epidermis are slightly smaller than the remainder and are sunk below the level of the epidermis. Because of their position and shape, which is slightly triangular compared with the rectangular cross-sections of the normal epidermal cells, they suggest the guard cells of stomata. They are found on sections at various levels of the axis, but are not of very frequent occurrence. It is possible that the small cells could have been formed fortuitously by indentation and squashing of the epidermis, but they occur only in pairs and only on those sections of the axis where the epidermis is well preserved. Moreover, the cells themselves do not appear to be squashed. Stomata have not been seen in surface view. In cross-section, the guard cells measure 28.6 by 23 μm on average (figure 26, plate 36).

The cortex is divided into two zones. The outer one is composed of two to four layers of thick-walled cells, which are radially alined. Wall thickness varies between 2.6 and 5.2 μm. (In fossil preparations such as these it is impossible to distinguish between sclerenchyma and collenchyma, so the cells are better described as having thick walls.) The outer cortical cells, rounded or angular in cross-section, measure 45 by 39 μm on average. They are at least 200 μm long and their end walls are oblique or transverse (figure 32, plate 36).

Occasionally in pyritized material, the outer wall of the outermost layer of cortical cells, together with the epidermis, have been eroded away. The adjacent walls of the cortical cells therefore project into the matrix, giving the surface an irregular or hairy appearance. This phenomenon might account for the hairs terminating papillae described by Heard (1927).

Transverse sections through the protuberances reveal somewhat variable anatomy (figures 8 and 9, plate 34). Not enough were seen to allow conclusions as to their actual structure to be drawn. In all cases, the outer cortical layer of thick-walled cells is continued across the protuberance. In some instances, the width of the layer and the regular alinement of the cortical cells remains unchanged, so that the layer bulges outwards and the base of the protuberance is filled with structureless pyrites, probably representing the inner cortex. In others the outer cortex cells, irregularly arranged, completely fill the protuberance. Sometimes a break is seen in the cortical layer, immediately below the apex of the protuberance.

Description of plate 36

Gosslingia breconensis, figures 26–33

Figure 26. Part of TS axis showing epidermis and outer cortical tissue. ? stoma is indicated by arrow. × 118. (69.64.G17–11.)

Figure 27. As for figure 26. × 118. (69.64.G17–5.)

Figure 28. TS axis with almost complete xylem strand. Note widest elements toward centre. Possible protoxylem is indicated by arrows. × 56. (69.64.G18–4.)

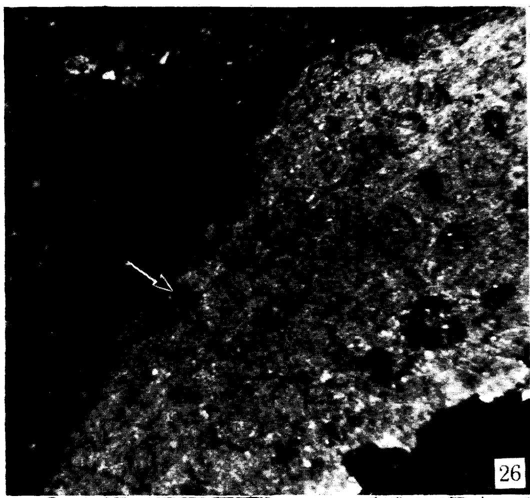
Figure 29. TS xylem strand surrounded by layer of compressed cells (arrows). × 118. (69.64.G19–3.)

Figure 30. Longitudinal section (LS) part of axis showing outer cortical tissue and xylem. × 118. (69.64.G20–4.)

Figure 31. Xylem strand recovered after maceration. × 360. (69.64.G16.)

Figure 32. LS part of cortex. × 118. (69.64.G21–6.)

Figure 33. TS ? rhizome. × 56. (69.64.G22–1.)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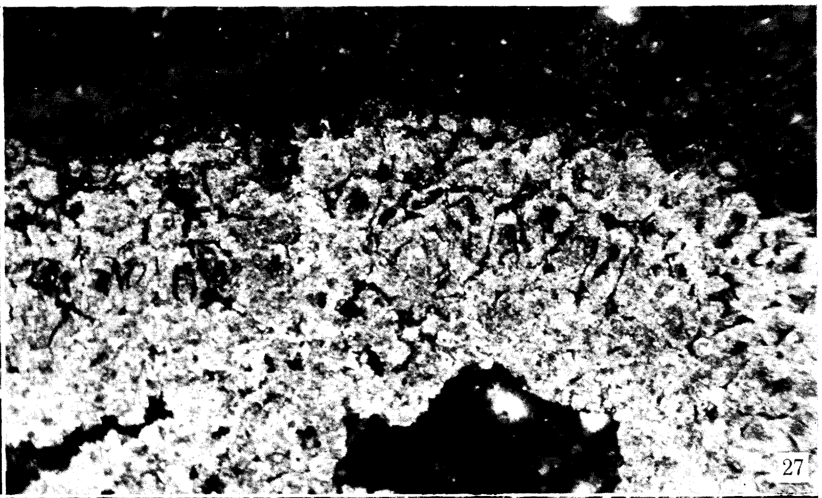
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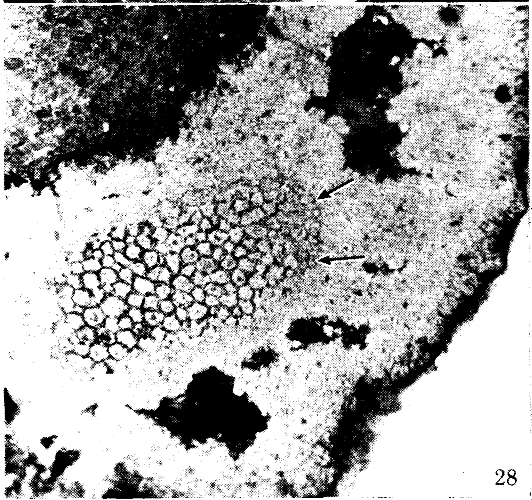
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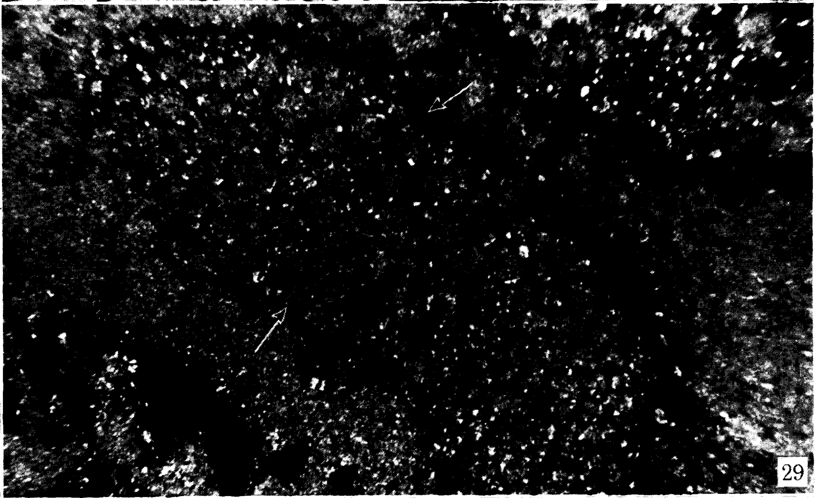
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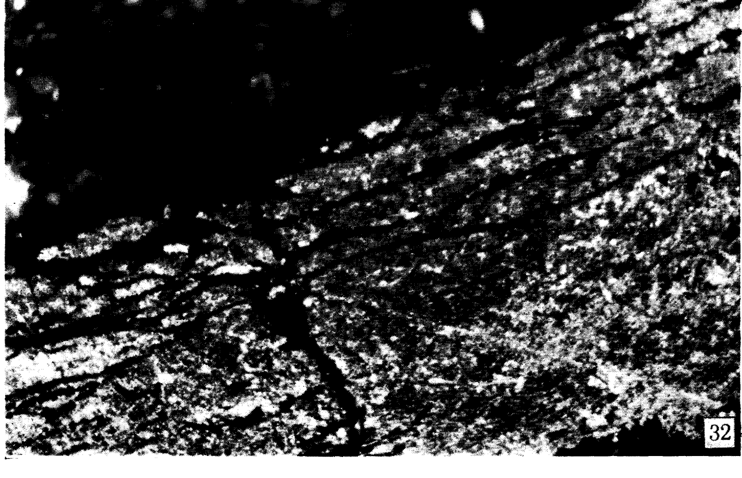
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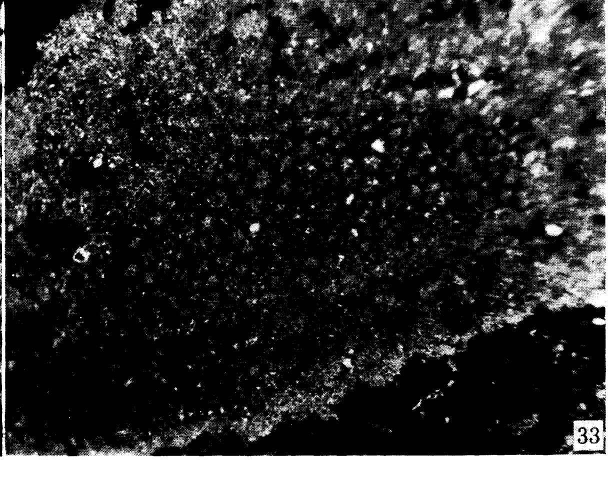
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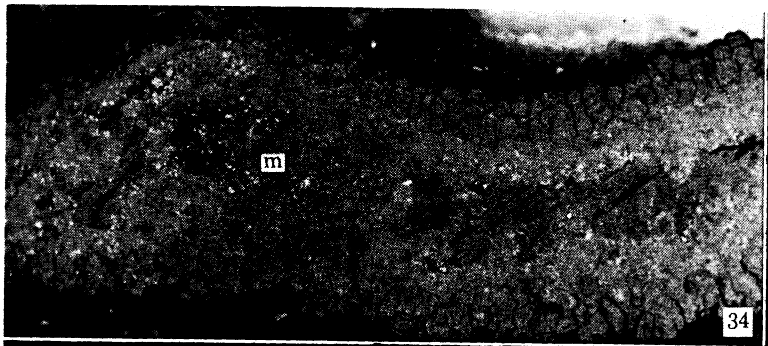

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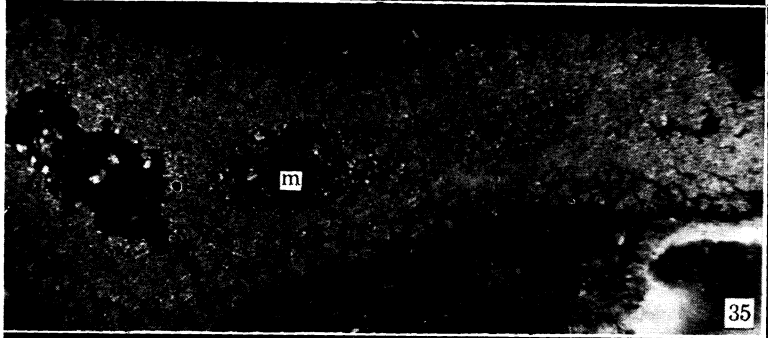

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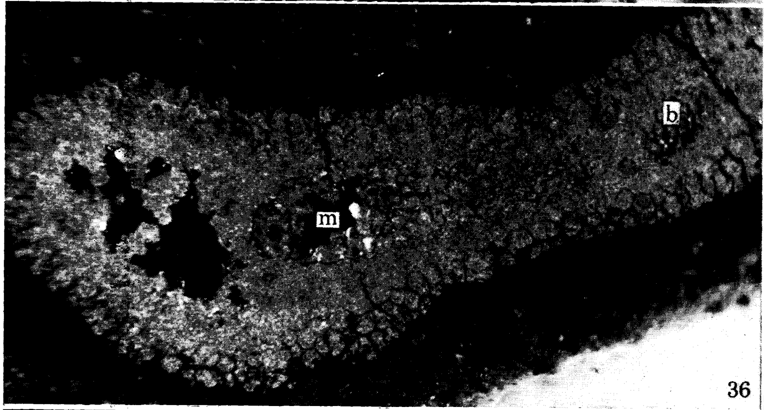

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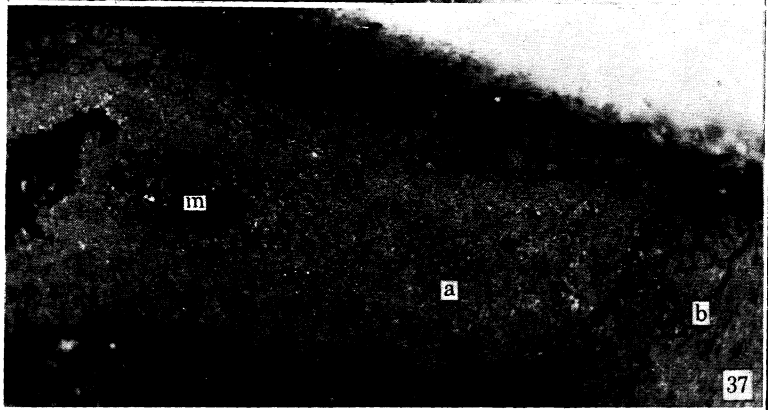

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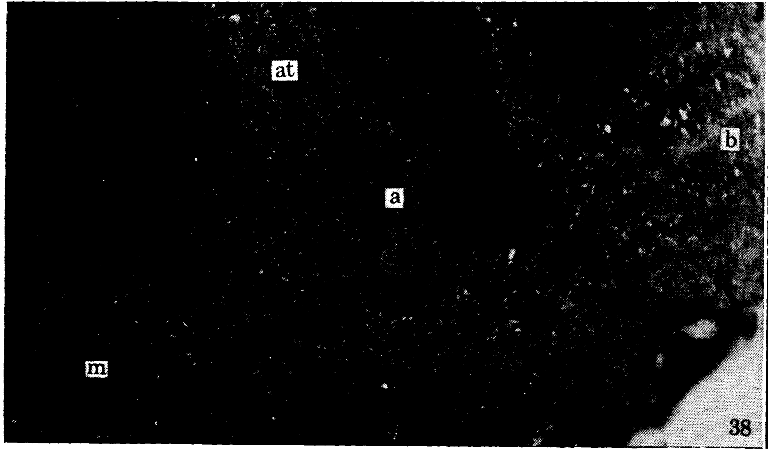

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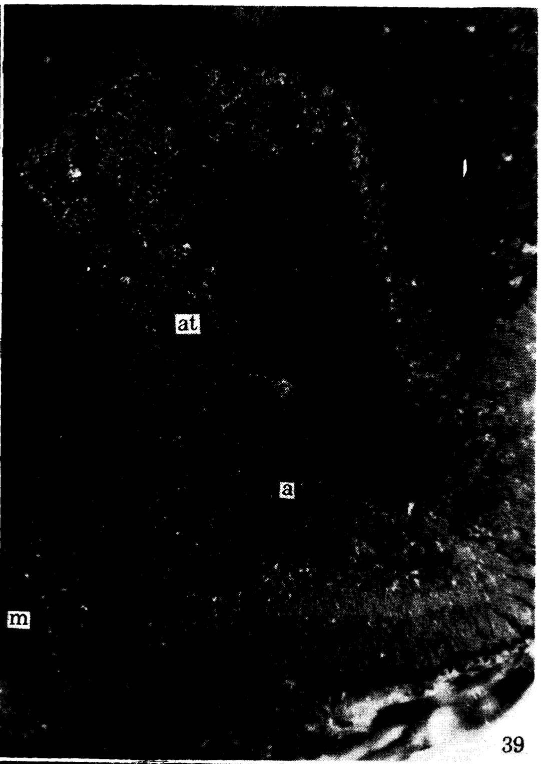

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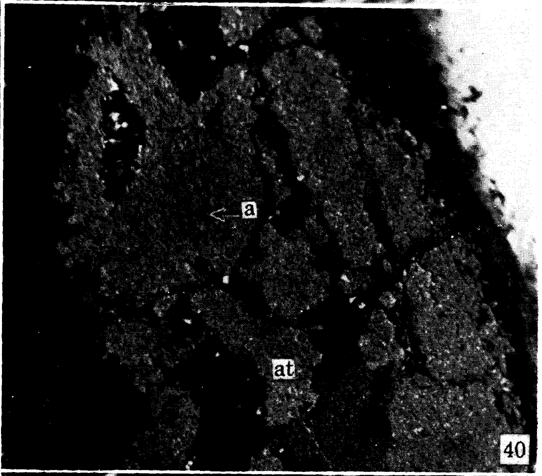

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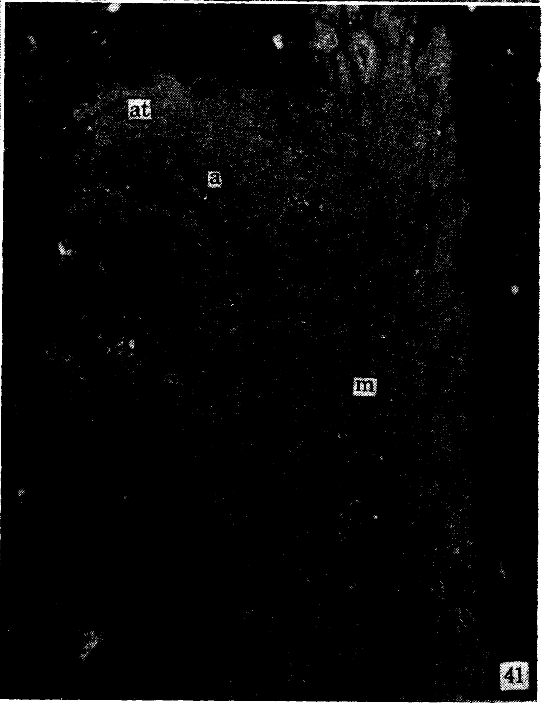

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The outer cortical tissue is continuous into the base of the axillary tubercle, but rather poorly developed (figure 41, plate 37). Here the long axes of the cells are parallel to that of the tubercle.

Cells are rarely preserved in the region of the inner cortex. Occasionally there is a suggestion of very small thin-walled cells in the region between the xylem and the outer cortex, but there is no good evidence to support it. The arrangement of pyrites in the sections gives the impression that there were some intercellular spaces.

No tissue, which could definitely be called phloem, has been seen. In some longitudinal sections, there is a region of striations outside the xylem, which could represent the phloem or perhaps poorly preserved protoxylem. Similarly, in certain transverse sections (figure 29, plate 36) a narrow region of crushed thin-walled cells surrounds the xylem. Again it cannot be said with certainty whether this is phloem or protoxylem.

The xylem strand is elliptical in cross-section. This shape is not produced from a circular one by compression, as the individual cells, on the whole, are not flattened and the number of cells across the major axis of the ellipse is greater than that along the minor. Compared with *Rhynia* and *Horneophyton*, the xylem strand is massive (figure 28, plate 36), its diameter being sometimes as much as half that of the stem. In cross-section, the xylem elements are, on average, 35 by 26 μm in diameter. The diameter of the cells in the cross-section does not vary greatly, but there is a slight decrease in size towards the periphery. At the periphery, there are small groups of cells which probably comprise the protoxylem (figure 28, plate 36). These have not been found in a band around the xylem, but this may be due to preservation failure. It may be said with certainty that the protoxylem is not central.

Longitudinal sections through the ends of the xylem elements show that they are tracheids, not vessels. The longest ones measured are 1015 μm. The tracheids usually exhibit scalariform thickening, but occasionally reticulate pitting is present (figures 30 and 31, plate 36). The actual thickening and pitting is best seen in sections which pass through a face of a cell. This usually occurs toward the end of the tracheid where it is cut obliquely. The lumen of the tracheid is filled with pyrites and the positions of the bars on two opposite sides of the cell are marked by dark spots. The spaces between the bars are rectangular in outline and are extremely regular in shape. The width of the bars varies between 1.3 and 2.6 μm and they are between 6.5 and 3.9 μm apart. Occasionally, when a polished section passes through the face of a cell, strands connecting the horizontal bars may be seen. Tracheids have also been recovered after maceration. Here, the distance between the bars is, on average, 6.5 μm and the width of the bars is 0.9 to 1.3 μm (figure 31, plate 36). These specimens indicate rather clearly that the thickening is scalariform, not annular or spiral. Reticulate pitting is sometimes seen in the macerated material.

DESCRIPTION OF PLATE 37

Gosslingia breconensis, figures 34–41

FIGURES 34 to 39. Series of transverse sections through an axis (69.64.G23 series) at a branching point. × 56.

FIGURE 34. Xylem strand before division. For explanation, see text. (m = xylem strand of main axis, b = branch xylem trace, a = axillary tubercle trace, at = axillary tubercle.)

FIGURE 40. TS axillary tubercle. × 56. (69.64.G24–1.)

FIGURE 41. LS axis and axillary tubercle. × 56. (69.64.G25–2.)

A series of sections taken through a single axis frequently include some which pass through a branching point. In all the specimens examined where this has occurred, branching is pseudomonopodial. The trace supplying the lateral branch is much smaller than that of the main axis and is irregular in shape.

The following sequence is seen in a series of sections starting just below the branching point and ending where the axis has divided into two. Plates 37 and 38 illustrate the stages described. The measurements given in brackets after each stage refer to the interval between that stage and the preceding one. They were obtained from a single axis by repeated grinding and then measuring with a micrometer.

A series of line drawings is given in figure 55. The numbers on the stages described below correspond to those on the individual drawings.

(i) The elliptical strand of xylem in the main axis becomes elongate and a constriction appears a short distance from one end of the strand [1.61 mm] (figure 34, plate 37, and figure 45, plate 38).

(ii) A small trace becomes separate from the main strand, at the end where the constriction appeared. This trace eventually supplies the lateral branch [0.89 mm] (figure 35, plate 37). In some axes, a second constriction appears before the branch trace separates off (figure 46, plate 38).

(iii) A second constriction occurs at the same end of the main trace as the first [0.55 mm] (figure 36, plate 37).

(iv) A second trace is produced so that at this level there are three distinct xylem strands. This second terete trace separates off in the direction of the axillary tubercle, which it eventually supplies [0.19 mm] (figure 47, plate 38). The lower part of the axillary tubercle is sometimes seen at this level (figures 38 and 39, plate 37). From a longitudinal section the angle of divergence of the axillary tubercle is 15° (figure 42, plate 38).

(v) Three xylem strands are seen again at this stage, but the axillary tubercle one is cut obliquely longitudinally or longitudinally and extends into the axillary tubercle where it ends abruptly [0.40 mm] (figure 43, plate 38). In a longitudinal section a bend of almost 90° from the original direction of the axillary tubercle trace is seen (figure 41, plate 37).

DESCRIPTION OF PLATE 38

Gosslingia breconensis, figures 42 to 53

FIGURE 42. LS axis showing separation of axillary tubercle trace. × 56. (69.64.G26–1.)

FIGURE 43. TS axis with LS strand to axillary tubercle. × 56. (69.64.G27–4.)

FIGURES 44 to 47. Series 69.64.G28 showing stages in division of the xylem up to the separation of the axillary tubercle trace. × 56.

FIGURE 48. Film pull of part of sporangium. × 135. (69.64.G12.) X = heavily carbonized border of sporangium. Spores are indicated by arrows.

FIGURES 49 to 53. Spores recovered from film pull of sporangium. (69.64.G13.)

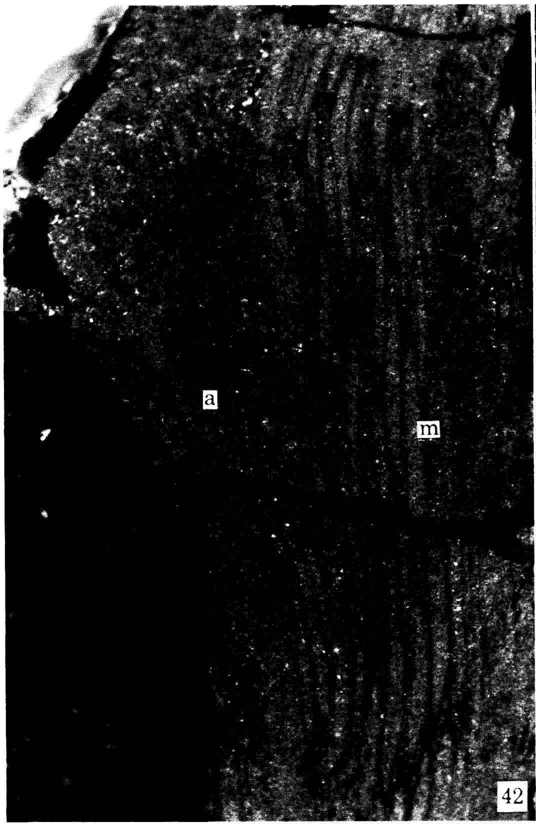
FIGURE 49. Part of exine of spore illustrated in figure 51 showing wall ornament. × 1000.

FIGURE 50. Two badly preserved spores. × 610.

FIGURE 51. Equatorial view of spore. × 610.

FIGURE 52. Part of exine, which is smooth, possibly in proximal region. × 1000.

FIGURE 53. Spores adhering to carbonized sporangium wall. × 610.



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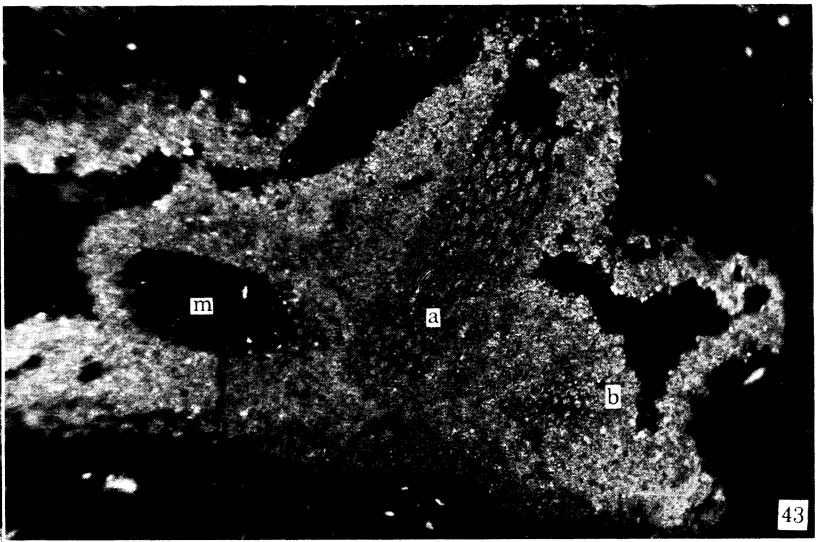

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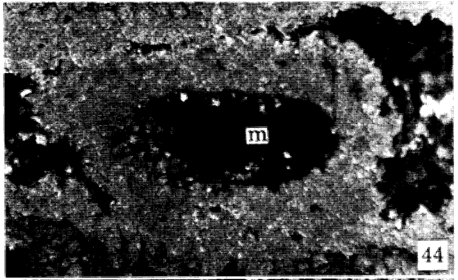

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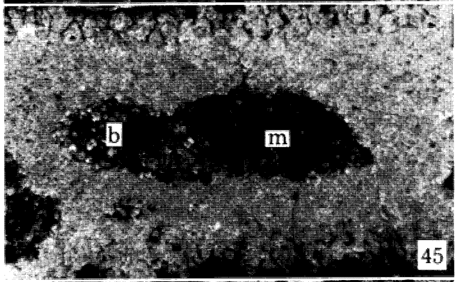

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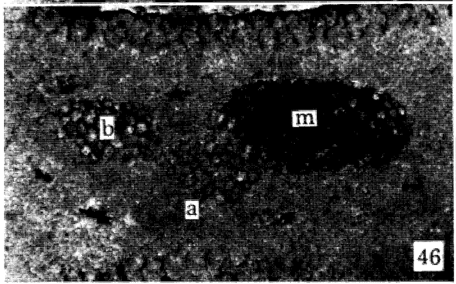

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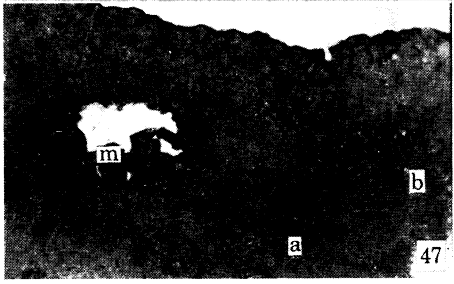

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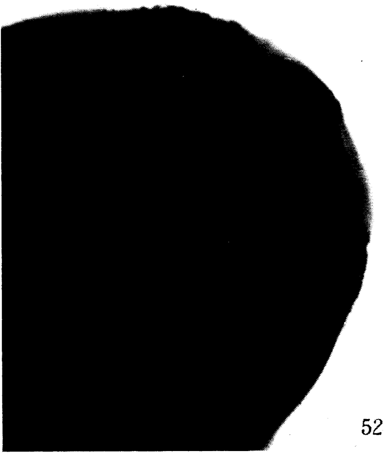
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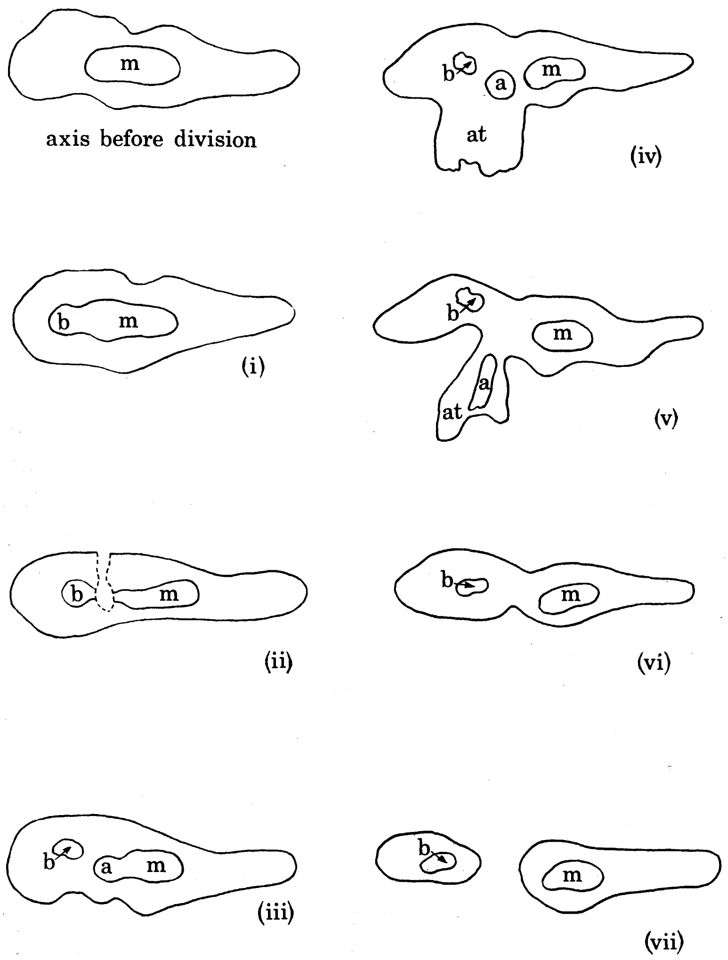
(vi) The axis itself divides into two unequally. The smaller branch is supplied by the smaller irregular trace. This division occurs 0.93 mm after the separation of the branch trace.

The series of sections presented in plate 37 shows the stages in the division of the xylem, but because of compression of the axis, though not of the traces themselves, the traces appear in a straight line. The series illustrated on plate 38 has therefore been included to show the relative positions of the xylem strands in an uncompressed axis.

The axillary tubercle itself projects at an angle of 90° from the main branching system. In longitudinal sections that include both the main axis and the tubercle, the latter sometimes has a slightly hooked appearance, the hook being directed downwards. The proximal part of the tubercle has an ensheathing layer of cortical cells, continuous with those of the main stem. The remainder is probably parenchymatous tissue. No definite cellular detail has been seen. Occasionally, traces of small, isodiametric cells are visible. No intact tissue has been found at the tip of the tubercle. In one specimen, the pyrites at the tip of the tubercle is slightly lobed in outline, perhaps representing large parenchymatous cells. The xylem strand entering the



axis before division

(i)

(ii)

(iii)

(iv)

(v)

(vi)

(vii)

Figure 55. Drawings of a consecutive series of transverse sections through an axis, showing the division of the xylem strand at a branching point. × 20. (69.64.G29.) m = xylem strand of main axis, a = xylem trace to axillary tubercle, b = xylem trace to branch, at = axillary tubercle. The numbers, (i) to (vi), correspond to those used in the text on pages 234 and 235.

tubercle is as much as a third the diameter of the tubercle and is circular in cross section (figure 40, plate 37). Frequently, the strand ends abruptly without tapering and often appears in contact with the surrounding matrix. This is due to failure of preservation of the tissue at the tip of the tubercle (figure 41, plate 37, and figure 43, plate 38).

One of the axes found in the same rock differs slightly from the remainder (Series 69.64.G 22) (figure 33, plate 36). Most noticeable is the absence of a thick-walled outer cortex. The arrangement of pyrites in the wide cortical region suggests that there are many intercellular spaces. There are also some thin dark lines in this region, which perhaps represent the walls of thin-walled cells. No epidermis is present. The appearance of the tissue to the margin of the specimen is uniform. The axis measures 2.5 by 1.1 mm in transverse section and the massive xylem strand, 1.03 by 0.4 mm. No axillary tubercle was found on the short length of axis examined.

Heard noted that the rhizome of *Gosslingia*, which he found attached to the aerial stems, had no thick-walled tissue in the outer cortex. This is the only reason for postulating that this different kind of axis is the rhizome. It shows none of the papillae or rhizoids described by Heard.

Attempts to elucidate details of the sporangium wall were, at first, unsuccessful. It was impossible to lift a complete sporangium from the rock, not because of carbon cleavage, but because the carbonized sporangium wall is closely adpressed to the rock grains, giving it a granular appearance. When the rock was removed on maceration, the sporangium fell apart. The thickened border around the sporangium was more easily removed. Clearing with Schulze's solution gave no cellular detail except for slight indentations at regular intervals on the outer margin. The stalk of the sporangium was also removed and cleared. Again no cellular detail is visible and no vascular tissue has been recovered. Film pulls (made by pouring peel solution, cellulose nitrate in amyl acetate, over the sporangium) were more successful (figure 48, plate 38). In some, cells can be seen in the sporangium wall. These are small and round to angular in outline. They measure approximately 20 μm in diameter. Occasionally spores can also be seen. Unfortunately the wall ornament in these cannot be seen properly as the film pull distorts the edge of the spore.

A small number of spores (12) were recovered by first dissolving such a film pull in amyl acetate and then by picking out the spores individually from the sporangium wall debris (figures 50 to 53, plate 38). In a few cases spores are found still attached to the sporangium wall fragments (figure 53).

These spores are variable in outline but mainly subtriangular ranging in diameter between 36 and 50 μm with a mean at 41.6 μm. Quite a high proportion are seen in equatorial view (figure 51). No triradiate marks were found. The exine ornament is variable, being composed mainly of spini, with some coni and bacculae (figure 49, plate 38). The majority have bases 0.5 μm in diameter and are 1 μm high, but some of the spines measure 2 μm high, while the truncated elements are 0.5 μm high. Very poor preservation often makes it difficult to distinguish between true ornament and structures produced by erosion of the exine. A large area of the spore appears to have little or no ornament.

Spores were also isolated by removing a sporangium from the rock and macerating it. The spores recovered were then cleared. Great care was taken that as few grains as possible remained attached to the sporangium, but some grains still adhered to the surface and were even found inside the sporangium itself. It is not surprising therefore that preparations made in this way were often found to be contaminated by dispersed spores.

5. DIAGNOSIS

Genus *Gosslingia* Heard, 1927 (see his page 203)

Emended diagnosis

Plant rootless and leafless. Gregarious erect axes cylindrical, dichotomously and pseudomonopodially branched, ? arising from dichotomously branched rhizomes with rhizoids. Stems circinately coiled in apical regions: surfaces of some axes with protuberances; large projections (axillary tubercles) occur below branching points. Axes have elliptical xylem strands composed of tracheids with scalariform and reticulate pitting; protoxylem exarch, ? xylem surrounded by phloem; axillary tubercles with vascular strands circular in cross-section. Outer cortex composed of many layers of thick-walled elongate cells. Epidermis with stomata. Stalked sporangia borne laterally at intervals over a definite fertile region. Sporangial shape variable ranging from reniform to globose, with heavily carbonized convex margin. Spores variable in shape, with part of exine smooth and part ornamented by spini, coni and bacculae.

Gosslingia breconensis Heard, 1927

Characteristics as described for the genus. Plant at least 50.0 cm high, with axes 0.5 to 4.0 mm wide. Dichotomous branching usually confined to apical regions. Majority of axes smooth, but some have small areas covered by protuberances of varying size, on average 244 μm long, 152 μm wide and 100 μm high. Axillary tubercles 1.36 to 0.38 mm long (average 0.84 mm), and 1.01 to 0.45 mm in diameter (average 0.64 mm), each supplied by terete xylem strand 0.22 to 0.12 mm diameter (average 0.17 mm). Xylem strand of main axis elliptical 798 to 363 μm by 363 to 174 μm in cross-section (average 576 μm by 247 μm), composed of scalariform and reticulate tracheids 45 to 10 μm in diameter; protoxylem exarch. Outer cortex composed of 2 to 4 layers of thick walled cells 87 to 29 μm by 72 to 29 μm (average 45 by 39 μm) in cross-section, up to 200 μm long. Sporangia borne laterally; 2.5 to 1.7 mm long, 2.2 to 0.9mm wide; on short stalks, 0.5 mm long and 0.4 mm wide. Plant apparently homosporous. Spores 36 to 50 μm diameter; part of exine ornamented with coni, spini and bacculae; majority 1 μm high, but spini up to 2 μm.

Lectotype—National Museum of Wales, no. 62.355.G9. This was figured by Heard on plate 15, figures 2 and 3.

Locality of lectotype—Brecon Beacons Quarry, Breconshire, South Wales, Great Britain.

Horizon of lectotype—Senni Beds, Breconian Stage, Lower Old Red Sandstone, Lower Devonian (≡Siegenian–Emsian).

6. AFFINITIES OF *GOSSLINGIA*

It is surprising that, in spite of the very thorough description of *Gosslingia* published by Heard in 1927, until quite recently it has been regarded as a plant of uncertain affinities about which little is known. Heard himself made little attempt to discuss the affinities of the plant, although he did think that it resembled *Rhynia* in some respects. In a discussion reported at the end of the paper, McLean suggested it was 'an early approach to the Botryopteridean fern' (p. 207). Edwards, however, thought that *Gosslingia* was related to the Rhyniaceae. The similarity of the reniform sporangia to those found in the new genus *Zosterophyllum* (also published in 1927) was commented on. Lang (1927) also referred to this similarity, while Seward in *Plant life through the* *ages* (1933) went as far as to suggest that *Zosterophyllum* and *Gosslingia* might have been the same plant.

It is important to note, when considering the discussion following Heard's paper, that before 1927 the best known simple Devonian plants, *Rhynia*, *Horneophyton*, *Asteroxylon*, *Psilophyton* and *Hicklingia*, were all thought to have had terminal sporangia and, therefore, had been placed in the class Psilophytales. [Although *Zosterophyllum* had been first described by Penhallow in 1892, it had been almost ignored until Lang's paper was published in 1927.] The Psilophytales had been erected by Kidston & Lang in 1917, who defined it as follows:

'This class is characterized by sporangia being borne at the ends of certain branches of the stem without relation to leaves or leaf-like organs.'

It was originally created to include *Rhynia Gwynne-Vaughanii* and certain specimens described under *Psilophyton*. As *Asteroxylon* was then thought to have terminal sporangia on naked axes, all the plants placed in the class before 1927 conformed strictly to the original diagnosis. In contrast, both *Gosslingia* and *Zosterophyllum* had lateral sporangia.

The importance of this difference in sporangia position has since been emphasized by Leclercq (1954) and Hueber (1964*a*). More recently, Banks (1968), in his new classification of the psilophytes, has those with lateral sporangia in a new subdivision of the Tracheophyta, the Zosterophyllophytina. The only order, the Zosterophyllales, contains two families, the Zosterophyllaceae and the Gosslingiaceae, with *Zosterophyllum* as the type genus in the former and *Gosslingia* in the latter.

I am not in complete agreement with Banks concerning this division into families. I propose to review almost all those plants he placed in the Zosterophyllophytina and to attempt an assessment of their affinities with *Gosslingia*. The Rhynie chert plants at present under investigation by Lyon and co-workers will be excluded from this account.

The close similarity in sporangial shape that *Zosterophyllum myretonianum* shares with *Gosslingia* has already been mentioned. Since 1927, further species of *Zosterophyllum* have been described (see Walton 1964; Edwards 1969) including *Z. llanoveranum* in which sporangia were borne in two rows on the fructification axis. Although sporangial shape was similar to that in *Gosslingia*, in *Zosterophyllum* species the lateral sporangia were aggregated into spikes of varying degrees of compactness. Another difference lies in the orientation of the two valves of the sporangium with respect to the fertile axis. It is of interest to note that one specimen of *Gosslingia* showed both types of orientation, this condition perhaps being brought about by twisting and folding of some of the sporangia during preservation. Anatomically *Gosslingia* and *Z. llanoveranum* are almost indistinguishable, both possessing thick outer cortices and exarch xylem strands, composed of scalariform tracheids. The xylem in *Gosslingia* was usually much more massive than that in *Zosterophyllum llanoveranum*, but it is possible that this is the result of only partial petrifaction of the xylem in *Z. llanoveranum*. Although it is very tempting therefore to conclude that the anatomy of the two genera *Zosterophyllum* and *Gosslingia* was very similar it is first necessary to consider whether the anatomy of *Z. llanoveranum* was typical of the genus as a whole, or whether the bilateral symmetry of the sporangial region of this species was reflected in the shape of the stele. It has already been pointed out in a report on *Z. llanoveranum* (Edwards 1969) that, in all but one of the axes examined, the vascular strands were elliptical, but that all such axes were found within or below the sporangial region. Whether or not the xylem strand was still elliptical further down the axis was not known with certainty but the terete strand described in *Z. llanoveranum* was found in an axis a few millimetres below the sporangial region. Obviously the shape of the xylem in those species with spirally arranged sporangia is of greatest importance to this discussion, but unfortunately, the anatomy of such plants as *Z. myretonianum* and *Z. australianum* is unknown. A further species of *Zosterophyllum*, at present under investigation in this laboratory, does have an almost circular protostele, while the sporangia, although appearing in two rows, are clearly spirally inserted on the fructification axis.

Zosterophyllum also differed from *Gosslingia* in that it did not possess axillary tubercles. *Z. myretonianum* and possibly *Z. llanoveranum* did exhibit H- + K-branching patterns, which were produced by successive dichotomies occurring close together. It will be recalled that the xylem strand to the axillary tubercle in *Gosslingia* was formed in a similar way. Indeed *Zosterophyllum* may perhaps be considered to exhibit a more advanced level of organization than *Gosslingia* with its sporangia confined to the distal regions of the plant and aggregated into definite fructifications and with a relatively complex branching system occurring only at the base of the plant.

As it is probable that *Bucheria* (Dorf 1933), another genus in which lateral sporangia are found in terminal fructifications, is congeneric with *Zosterophyllum*, it will be omitted from this discussion.

Banks & Davis (1969) described a plant from the Emsian of the Gaspé, which they named *Crenaticaulis verruculosus*. This new plant when looked at with the naked eye seems almost identical with *Gosslingia* except that it was larger and the margins of the axes were slightly irregular. Both plants had prominent axillary tubercles. Anatomically they also appeared similar. The arrangement of sporangia in both varied considerably, but the tendency for them to be opposite pairs was more pronounced in *Crenaticaulis*. Reniform sporangia, though common in *Gosslingia*, were rarely seen in *Crenaticaulis*. The two genera also differed in sporangial dehiscence (the sporangia in *Crenaticaulis* splitting into two unequal parts), in the anatomy of the epidermis, and in the presence or absence of teeth. Although two rows of teeth were also present on axes of *Crenaticaulis*, the emergences seen only occasionally in *Gosslingia* were not regularly arranged.

The Upper Devonian plant ('*Serrulacaulis*') which Hueber (1961) described and *Psilophyton princeps* var. *ornatum* (see Hueber 1964*a*, *b*, 1968; Hueber & Banks 1967) will be taken together as they both differed from *Gosslingia* in having very well-developed emergences, although the morphology of these was not the same in the two genera. In *P. princeps* var. *ornatum* the spines were glandular, while in the other plant the conical emergences were sometimes terminated by clusters of hairs. Both had globose, never reniform, sporangia. Although no definite fructifications were present, the sporangia in neither plant were scattered randomly over the branching system, but tended to be found only in the distal regions. It is therefore concluded that these two plants were not so closely related to *Gosslingia* as was *Crenaticaulis*.

Stolbergia spiralis (Fairon 1967) is also relevant to this discussion. Like *Gosslingia* it had an exarch xylem strand composed of scalariform tracheids, but in the absence of the fertile parts the two genera cannot be satisfactorily compared.

Returning now to Banks's classification in which *Gosslingia*, *Psilophyton princeps* var. *ornatum* and '*Serrulacaulis*' are placed in the same family, it has been shown that they, together, with *Crenaticaulis* are basically similar in having scattered lateral sporangia. It would obviously be unwise to suggest close relationships on the basis of this character alone. They did indeed have certain other morphological and anatomical features in common. All possessed elliptical xylem strands with exarch protosteles. In all, dehiscence was distal by a line around the sporangium which divided it into two equal or unequal halves. There were also differences, the most striking of which was the presence or absence of spines. A series may be traced from *Gosslingia* which was naked, through *Crenaticaulis* where small teeth were present and ending in *Psilophyton princeps* var. *ornatum* which had spines. Sporangial shape was variable. Axillary tubercles were present in only *Gosslingia* and *Crenaticaulis*, except for one record of a tubercle in *Psilophyton princeps* var. *ornatum* by Lang in 1932.

In placing all the above genera in the one family, the Gosslingiaceae, as Banks did, there is a danger that this family will become a dumping ground for all plants with scattered lateral sporangia regardless of their natural relationships. I believe, therefore, that only *Crenaticaulis* should remain with *Gosslingia* in the Gosslingiaceae, while the remaining genera should either be placed in a new family or left under the heading Incertae sedis.

7. STRATIGRAPHIC OCCURRENCE OF *GOSSLINGIA*

A few of the many localities in Breconshire and Monmouthshire at which *Gosslingia* is found are given by Croft & Lang (1942). I have been privileged to look through Croft's field notes, where many more localities are recorded. Indeed Croft appeared to consider the easily identifiable axes of *Gosslingia* as indicator fossils for the Senni Beds. Certainly, *Gosslingia* has not been found in the rocks immediately below (Dittonian) or above (Brownstones) which are relatively unfossiliferous in this area. A Dittonian flora from the neighbouring Welsh Borderland is at present being looked at in this laboratory. So far it has yielded fertile *Zosterophyllum llanoveranum*, but not *Gosslingia*. Up to the present time, *Gosslingia* has not been reported outside South Wales.

Croft thought that 'both the fauna and flora of the Senni Beds and their stratigraphical position show that they may be broadly correlated with beds as Siegenian-Emsian' (Croft 1953, p. 431).

This correlation still holds true today, but it should be emphasized that since 1953 many of the plant species present are known to have had much greater vertical ranges than was originally thought. Of the plants from the Senni Beds listed below, *Drepanophycus spinaeformis*, *D.* cf. *gaspianus* and *Psilophyton princeps* var. *ornatum* also occur in Upper Devonian, *D.* cf. *spinosus* in Middle Devonian and *Z. llanoveranum* in Gedinnian (Dittonian) rocks.

Drepanophycus spinaeformis
D. cf. *gaspianus*
D. cf. *spinosus*
Zosterophyllum llanoveranum
Z. cf. *australianum*
Psilophyton princeps var. *ornatum*
Dawsonites arcuatus
Sporogonites exuberans
Sciadophyton steinmanni
Krithodeophyton croftii
Cooksonia sp.
Taeniocrada sp.
Prototaxites sp.
Nematothallus sp.
Pachytheca sp.

Thus taking into account first, the vertical ranges of some of the species present and secondly, the fact that an identical assemblage is not known from elsewhere, it is concluded that any correlation based on the macro-flora alone would be unreliable.

8. General discussion of axillary tubercles

One of the most interesting features in *Gosslingia breconensis* is the small projection, called the axillary tubercle, below each branching point. This structure is not confined to the above genus, and has been reported on many other occasions on plants from Lower and Middle Devonian rocks. The following is an account of these records together with some comments on the possible nature of the axillary tubercle.

The term was introduced by Høeg (1942), when he described a circular scar occurring just below a dichotomy on an axis of *Hostinella* (for nomenclatural considerations, see Banks 1967) from the upper Middle Devonian of Spitzbergen. Such structures, often taking the form of a protuberance or depression, have been found on Lower Devonian fossils also, again usually on axes of *Hostinella*. The first record is found in Potonié & Bernard (1904), who described *H. hostinensis* from the Middle Devonian of Bohemia, as having 'sur les axes de divers ordres, d'empreintes particulières rappelant un peu la trace que pourrant laisser un bourgeon'. (pp. 16–17). Since then examples of *Hostinella* with tubercles have been recovered from the Lower and Middle Devonian of Scotland (Lang 1925) and from the Lower Devonian of France (Carpentier 1930), and Australia (Lang & Cookson 1927, 1930; Cookson 1935, 1949).

Hostinella is a form genus for sterile naked, dichotomously or pseudomonopodially branching axes (Halle 1916) which may or may not have axillary tubercles. The possession of such tubercles by different populations, however, does not necessarily imply relationships between them. The affinities of *Hostinella* with and without tubercles are essentially unknown and attempts to trace them have often given rather misleading results. For example, the *Hostinella* of Potonié & Bernard was renamed *Protopteridium* by Kräusel & Weyland (1933), but it must be emphasized that the sterile axes with tubercles were never found attached to the fertile axes of *Protopteridium* and that these fertile axes had no axillary tubercles. Although it is probable that some of the naked axes described by Potonié & Bernard did belong to *Protopteridium*, it is unwise to conclude that *Protopteridium* had axillary tubercles. Similarly Lang (1925) described *Hostinella* axes with axillary tubercles, associated with fertile axes, which he called *H. thomsonii* and *H. pinnata*. The fertile axes were later transferred to the genus *Milleria* (Lang 1926) and then to *Protopteridium* (Kräusel & Weyland 1938) again giving rise to the misconception that *Protopteridium* had axillary tubercles even though Lang had emphasized that sterile *Hostinella* with tubercles was never found attached to the fertile axes and that there were no tubercles on the fertile axes themselves. Lang also stressed that the use of the name *Hostinella* for the fertile axes was a provisional one as he did not want to increase the number of meaningless genera.

Høeg's assumption that *Asteroxylon* had axillary tubercles had a similar foundation. *Hostinella* with typical projections was described from the Middle Devonian of Germany by Kräusel & Weyland (1923). Later they assigned this plant to the new species, *Asteroxylon elberfeldense*, because they found the 'leafy' axes of *Asteroxylon* in association with the naked *Hostinella* axes (Kräusel & Weyland 1926). A recent paper by Fairon (1967) has shown that some of the latter belong to a new genus, in which the axes were not naked, but bore spirally arranged appendages.

Henderson (1932) described a *Psilophyton* flora from the Callander district of Perthshire. Associated with typical spiny *Psilophyton princeps* var. *ornatum*, he found both narrow and wide branch systems bearing axillary tubercles. These branches were smooth, but Henderson thought that any spines originally present could have been destroyed by the coarse sediment. In the absence of any trace of spines in these specimens this seems unlikely. Lang (1932) also examined fossils from this area and found a fragment of *Psilophyton princeps* var. *ornatum*, which had an oval depression just below a branching point. If this was indeed an axillary tubercle, then it is the only record of the structure on spiny *P. princeps* var. *ornatum*, although tubercles have also been reported on *P. goldschmidtii* by Ananiev (1960).

To complete this survey, *Gosslingia* and *Crenaticaulis*, already described in the above account, should be mentioned.

The morphological nature of the axillary tubercle has been the centre of much discussion. In 1904, Potonié & Bernard though it was a kind of bud, produced by two successive dichotomies, with one of the branches having aborted. They cited the position of the bud, exactly at the base of the two branches as evidence for this hypothesis. Lang & Cookson (1930) agreed with this interpretation. They pointed out that as the tubercle was axillary, it could not have been produced by a trichotomy and again suggested that they were 'rudimentary or dormant axillary branches' (p. 138). Zimmermann (1930), however, argued that the use of the word, bud, was misleading and suggested that the structure could have been a water-containing organ comparable to the ligule of lycopods. Høeg (1942) and Cookson (1949) described a tubercle as the base of an additional branch found below a branching point.

The first conclusively illustrated example of a branch, 7 mm long, in the position of an axillary tubercle is given by Banks & Davis (1969) in *Crenaticaulis*. Evidence for its being vascularized is given in this paper. Although in *Gosslingia* the axillary tubercles were merely small projections from the axis (the longest measured only 1.32 mm) each was supplied by a vascular strand, the diameter of which was much greater than that of the lateral branch. The vascular strand of the main axis underwent a double pseudodichotomy with the tubercle trace being formed by the second one. The trace ended abruptly without tapering, sometimes being in direct contact with the rock matrix.

The hypothesis that the tubercle was a dormant bud (i.e. a naked apical meristem) is still valid, but the possession of such a well-developed vascular strand is against this. It is perhaps more likely that the tubercle represented the base of a branch, which was either abscissed before preservation or was lost during preservation, because it projected at right angles to the branching system. Certainly it was more than a branch scar. Banks & Davis postulated that the structure was the base of a rhizophore comparable to that found in *Selaginella*.

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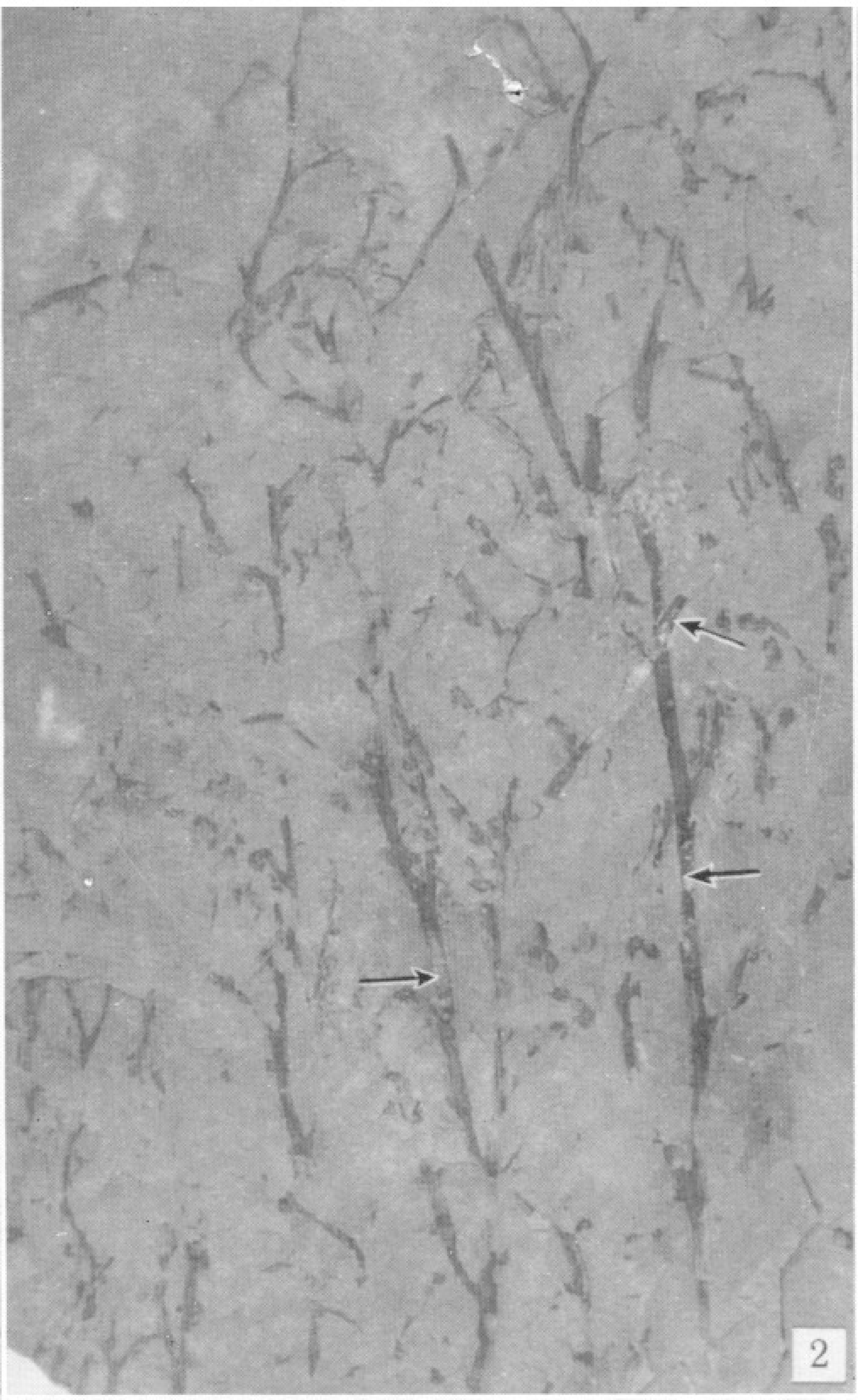
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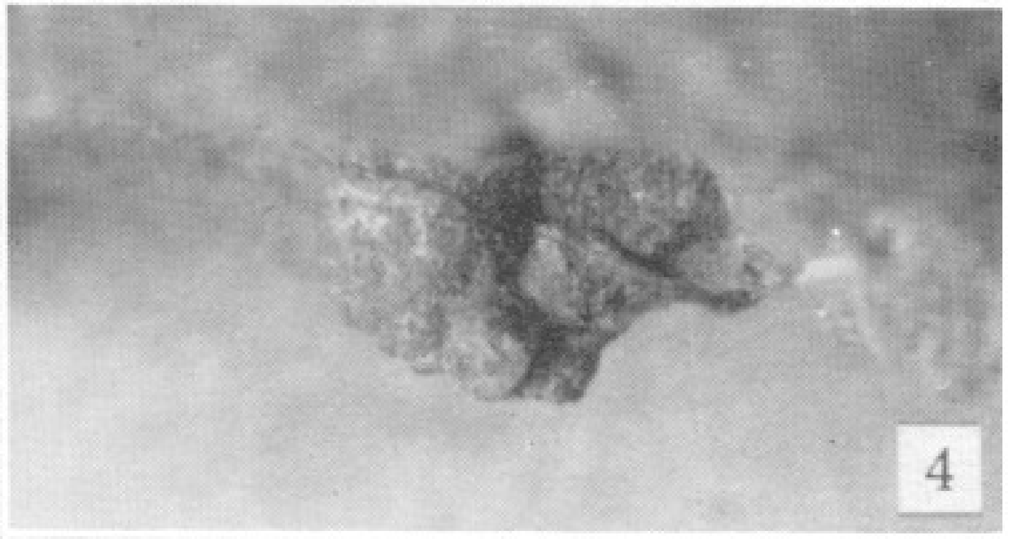
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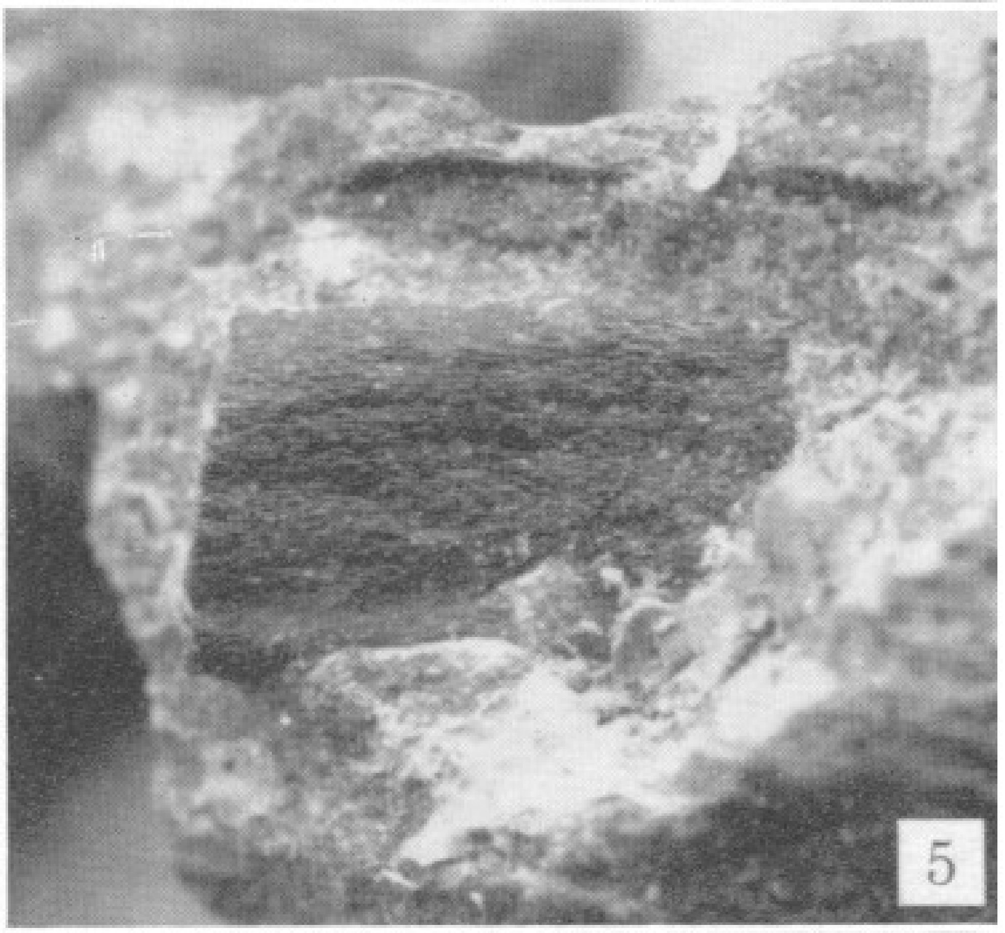
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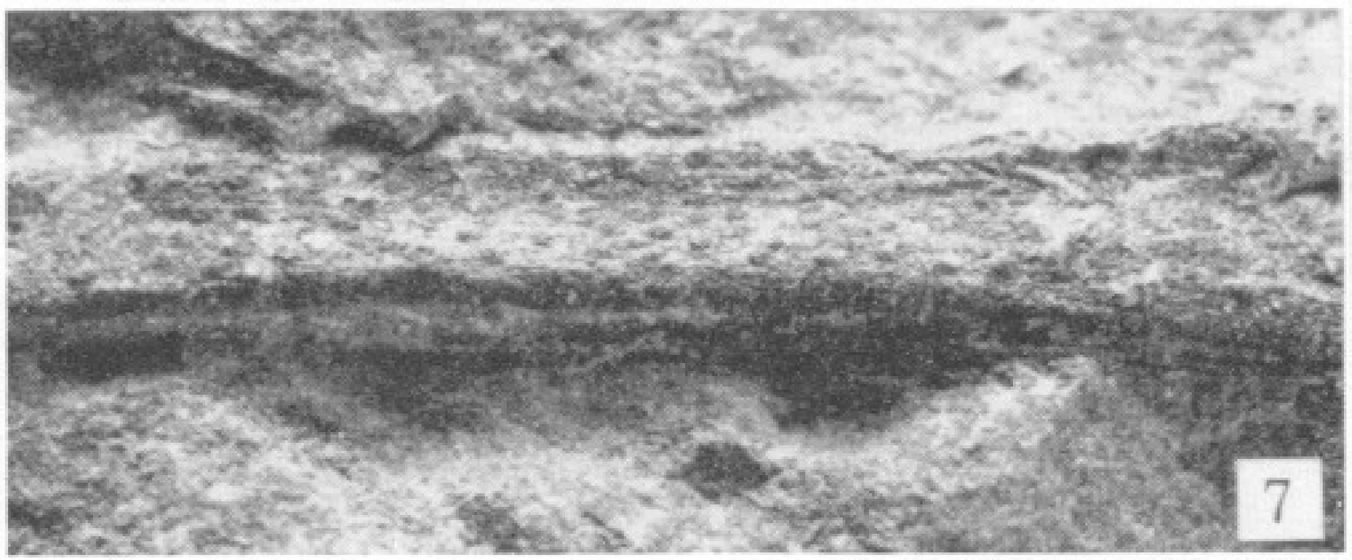
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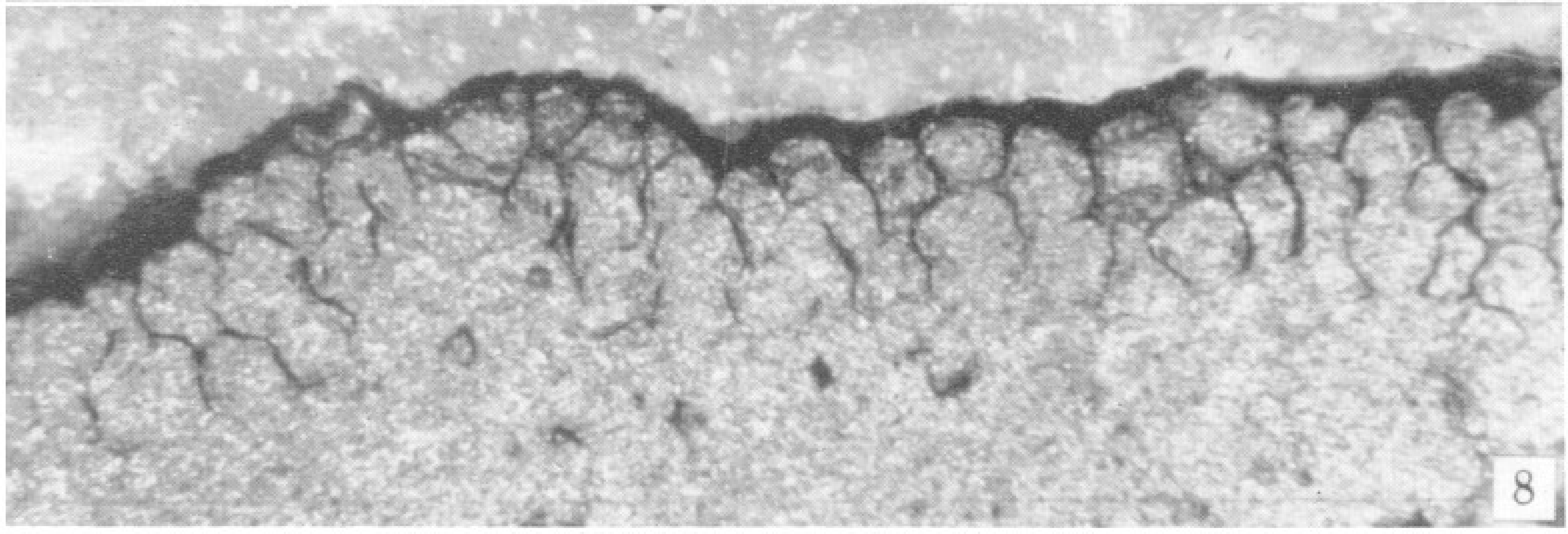
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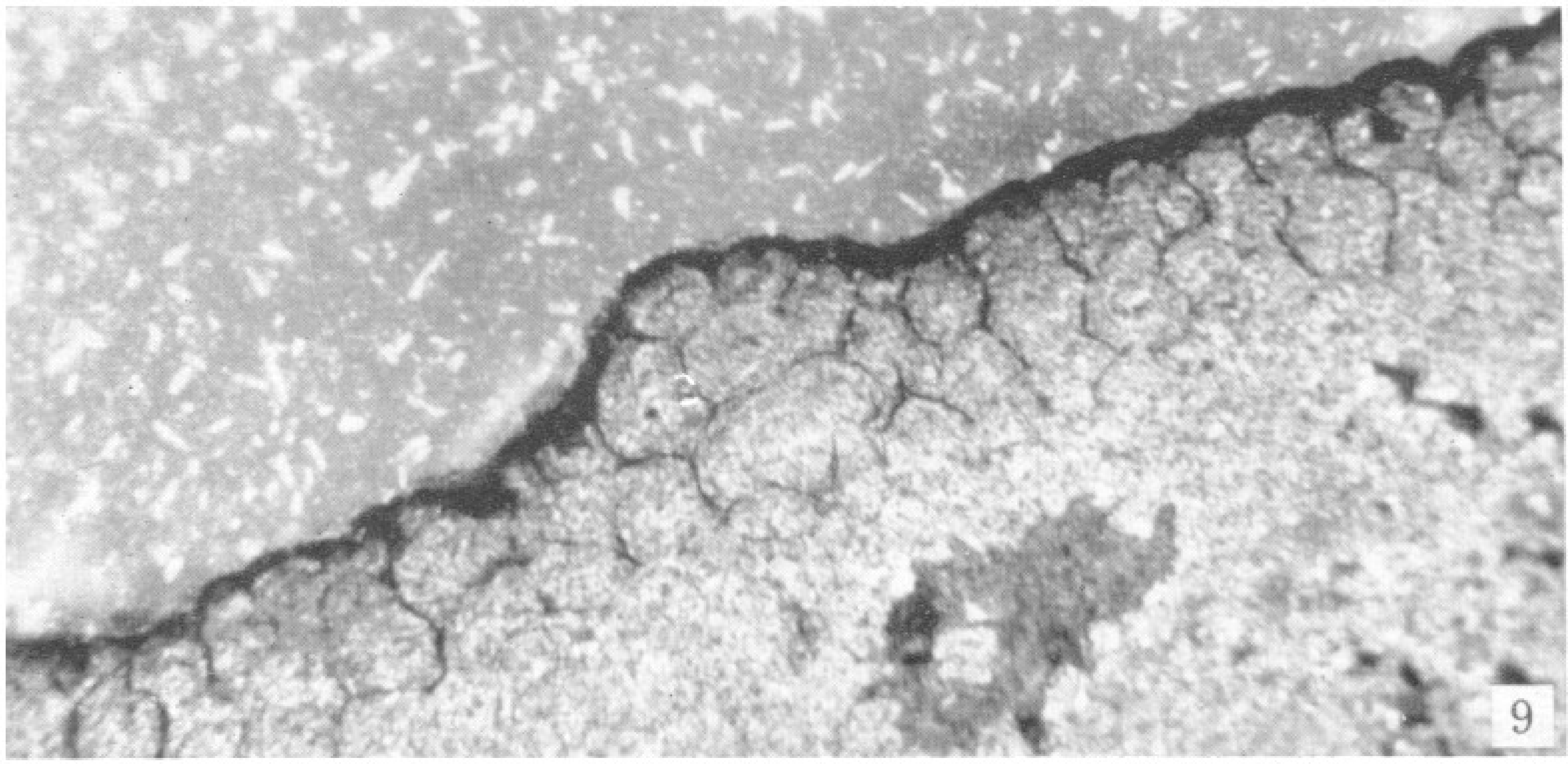
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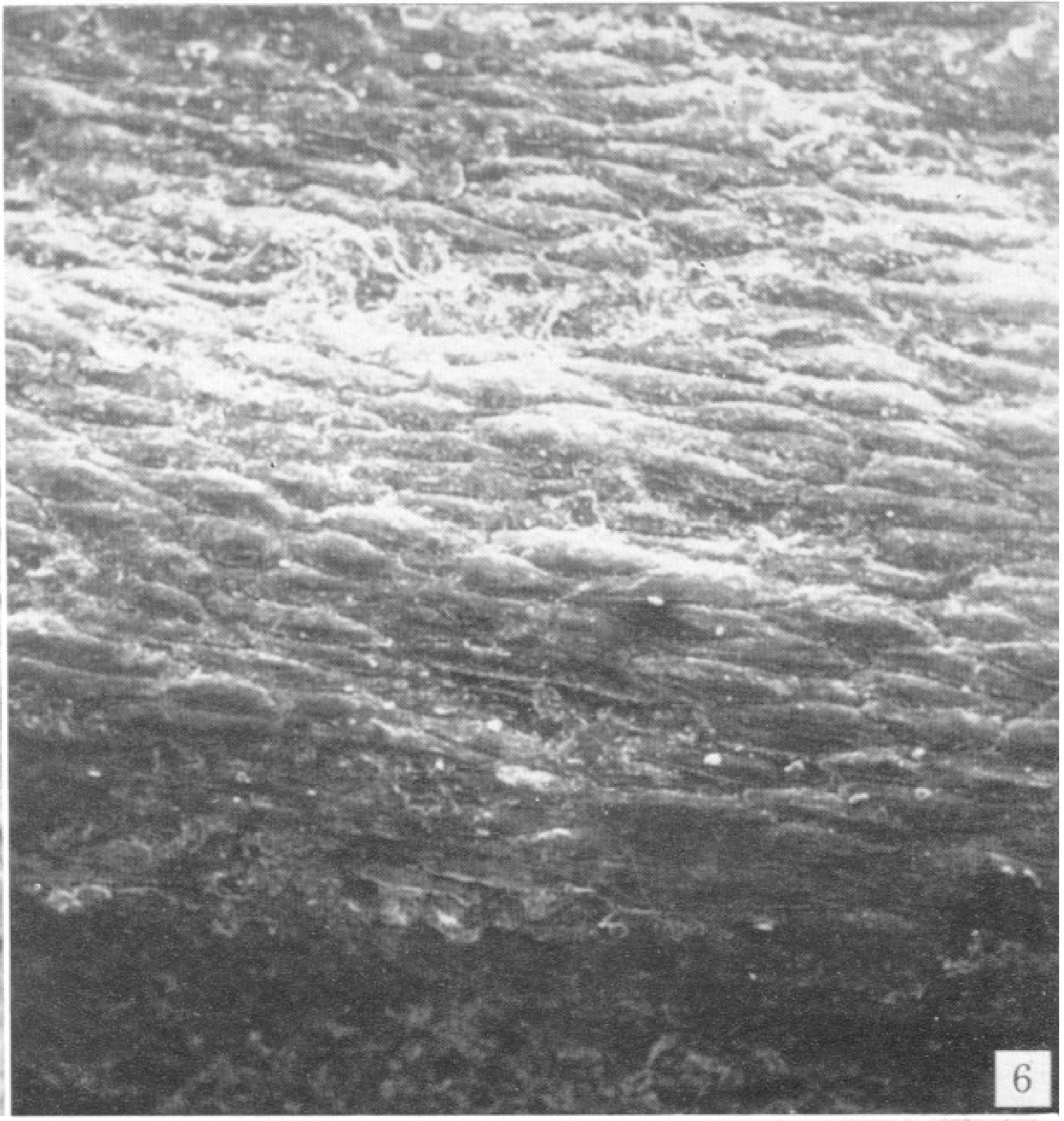
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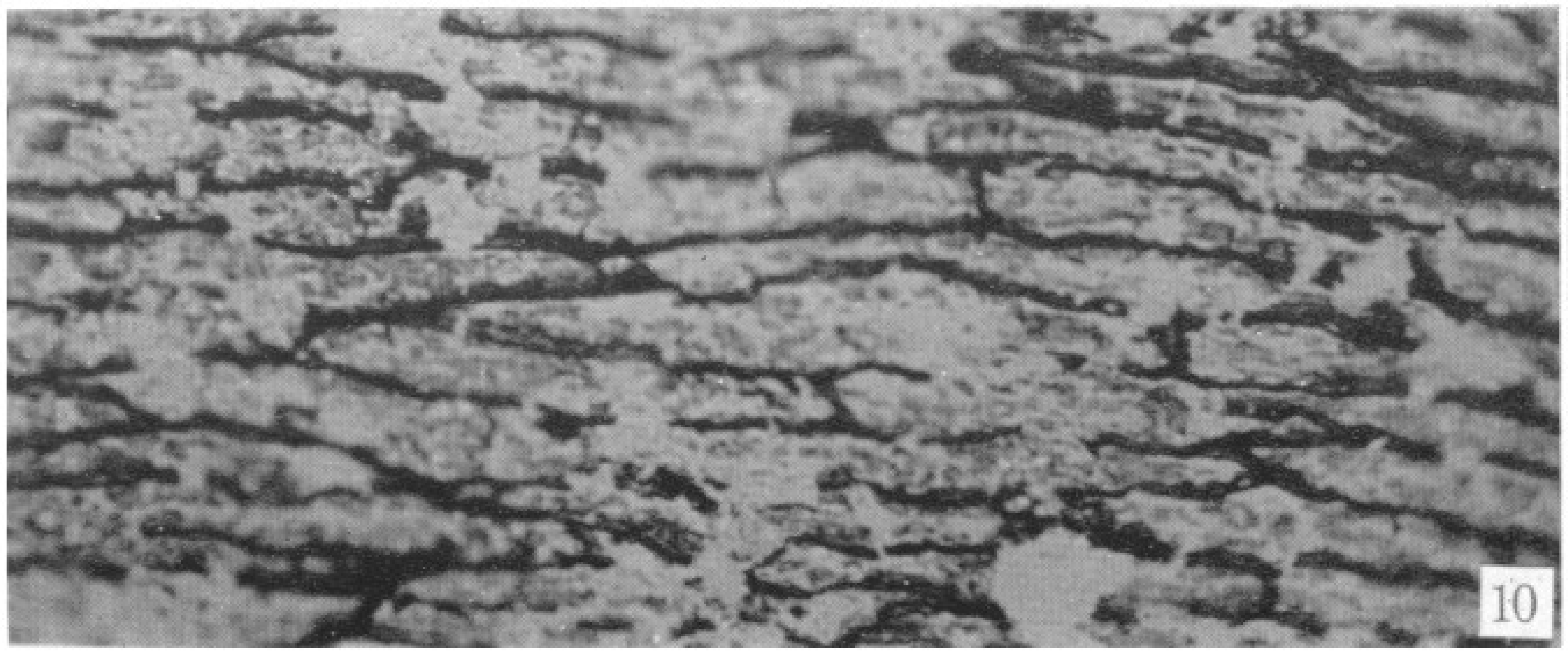
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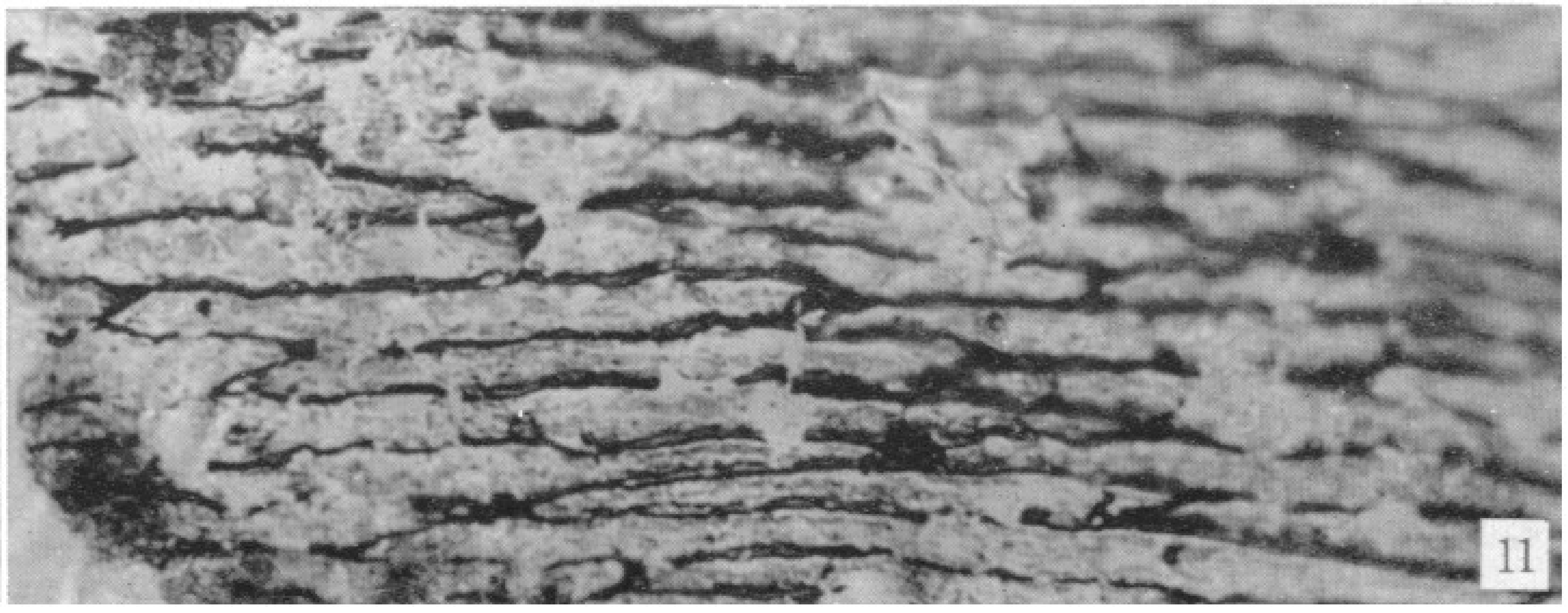
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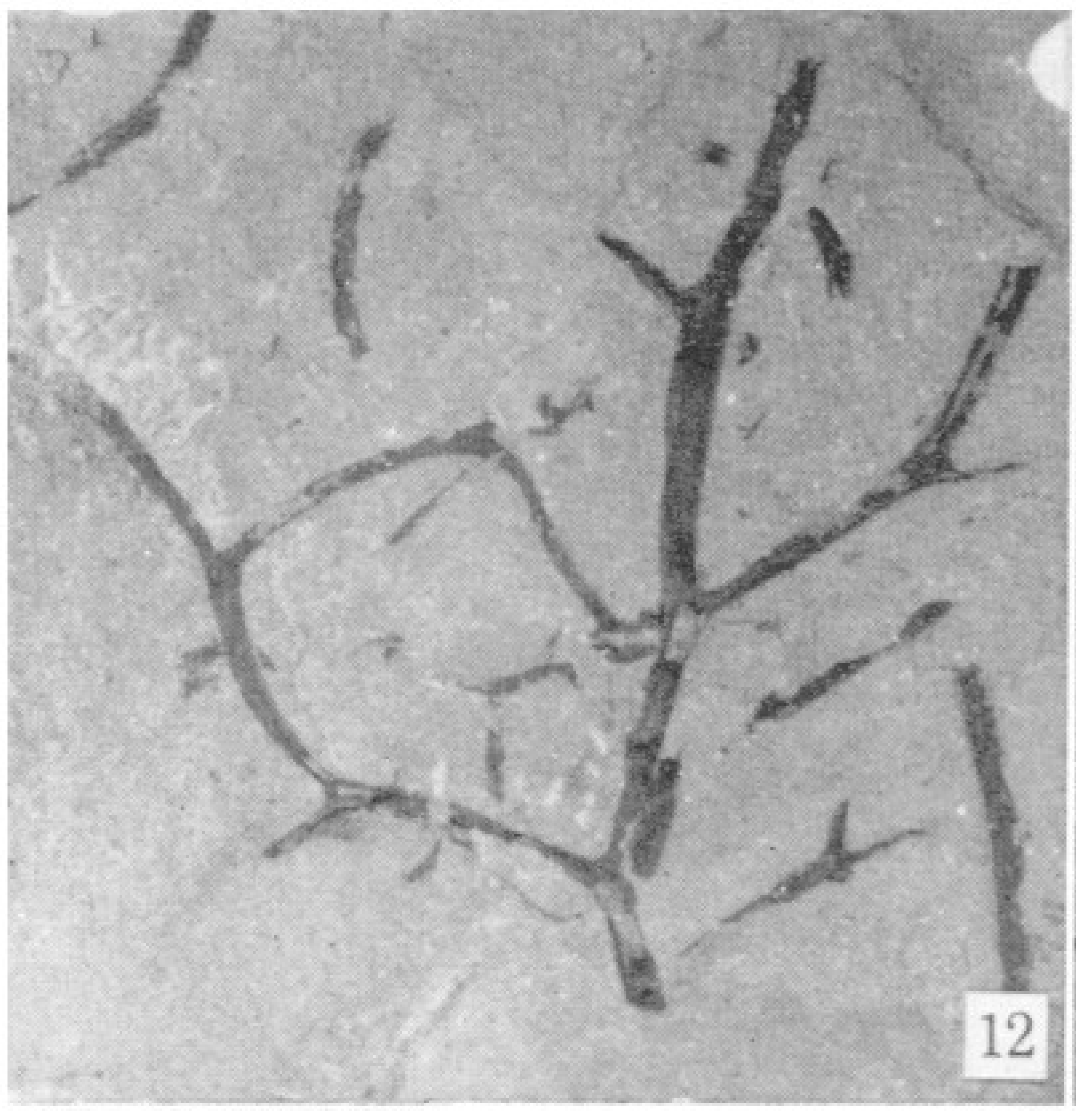
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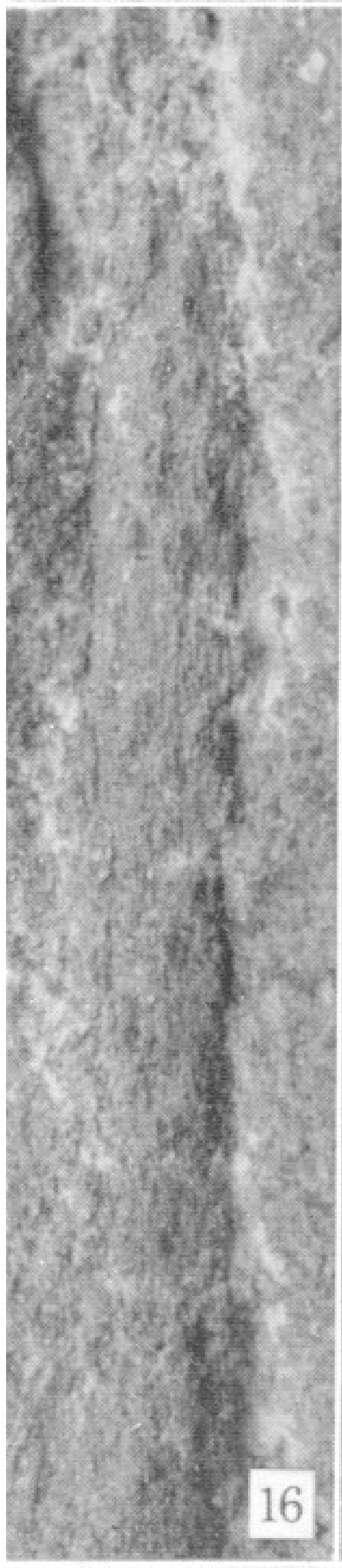
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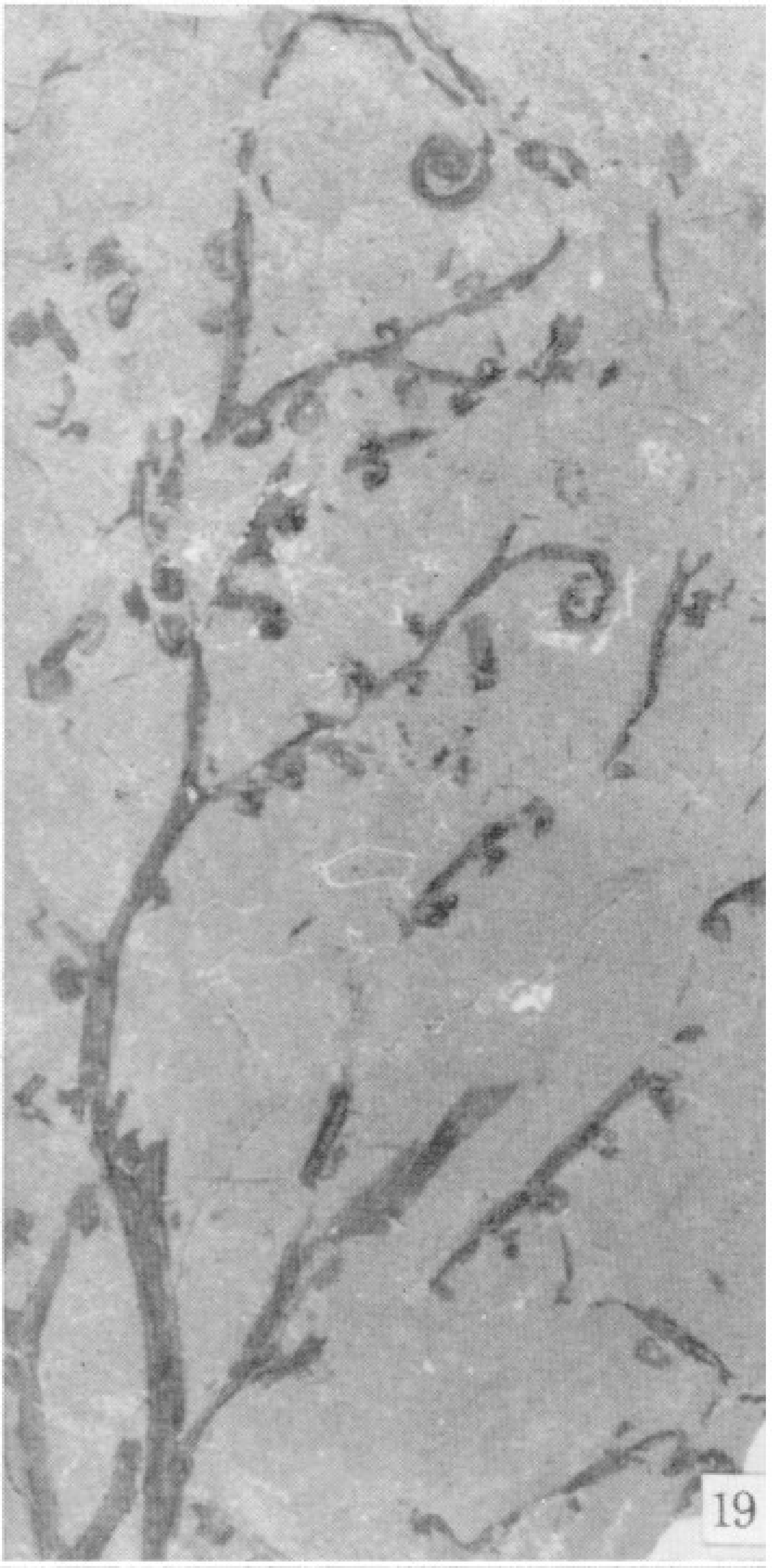
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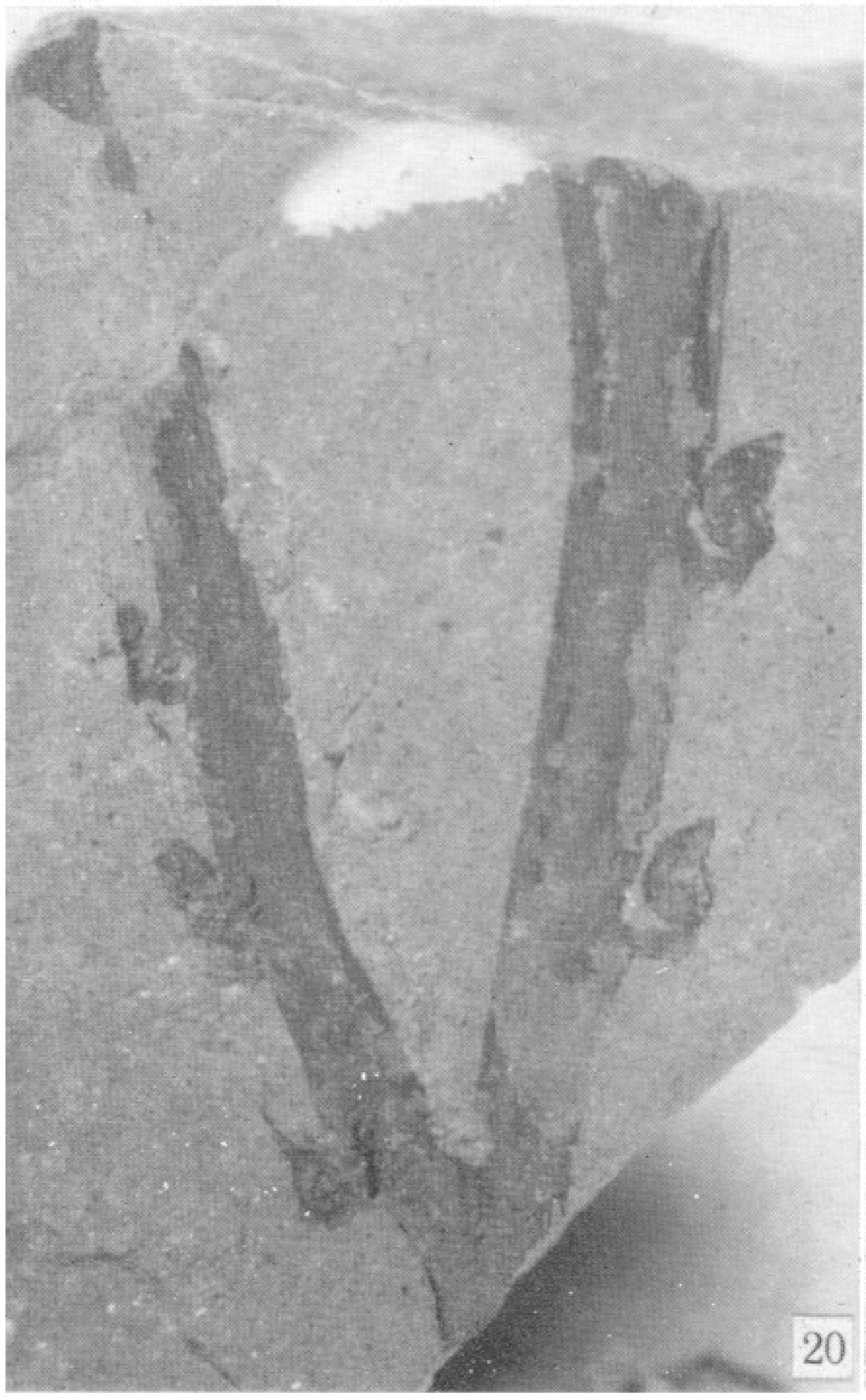
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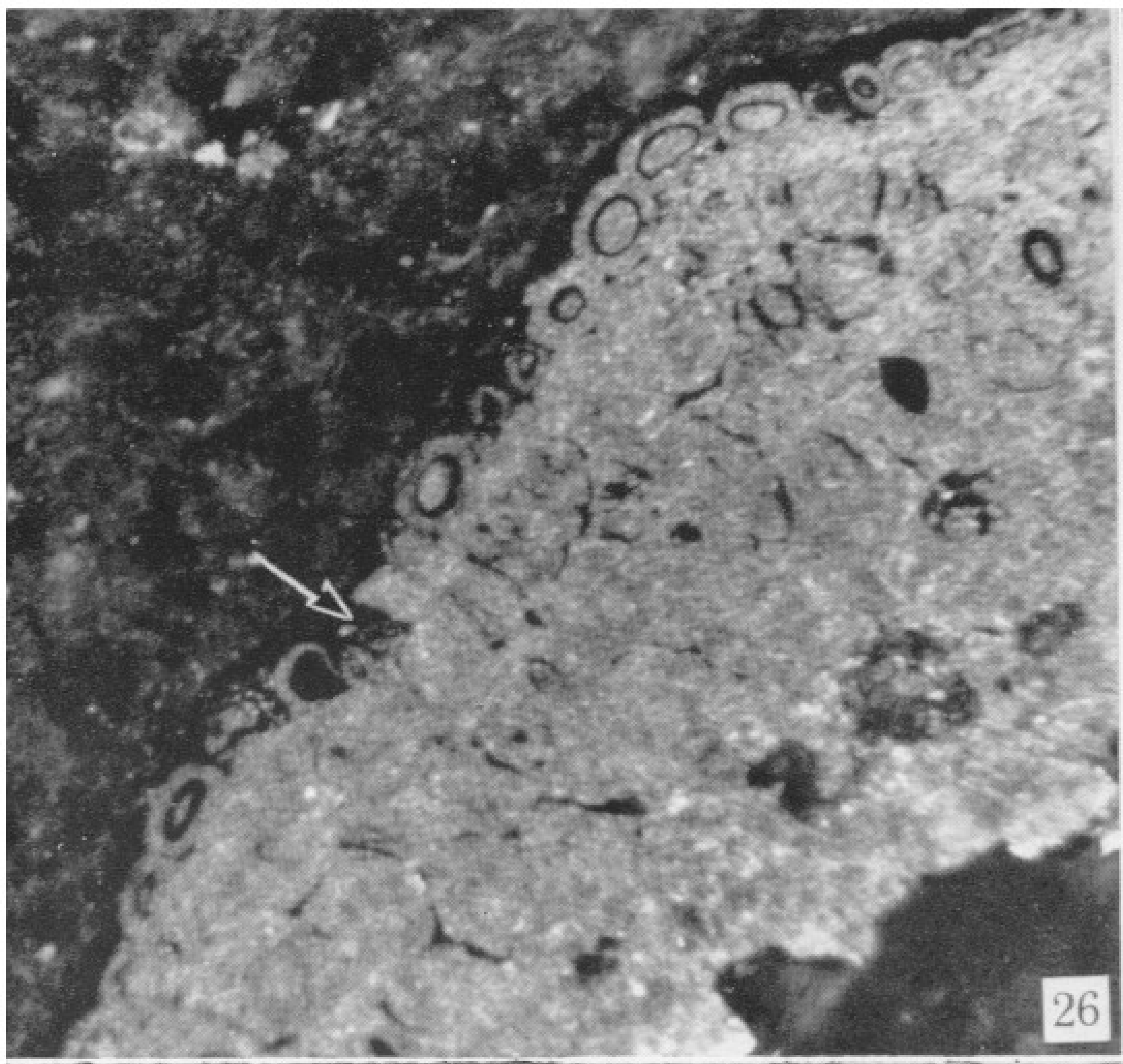
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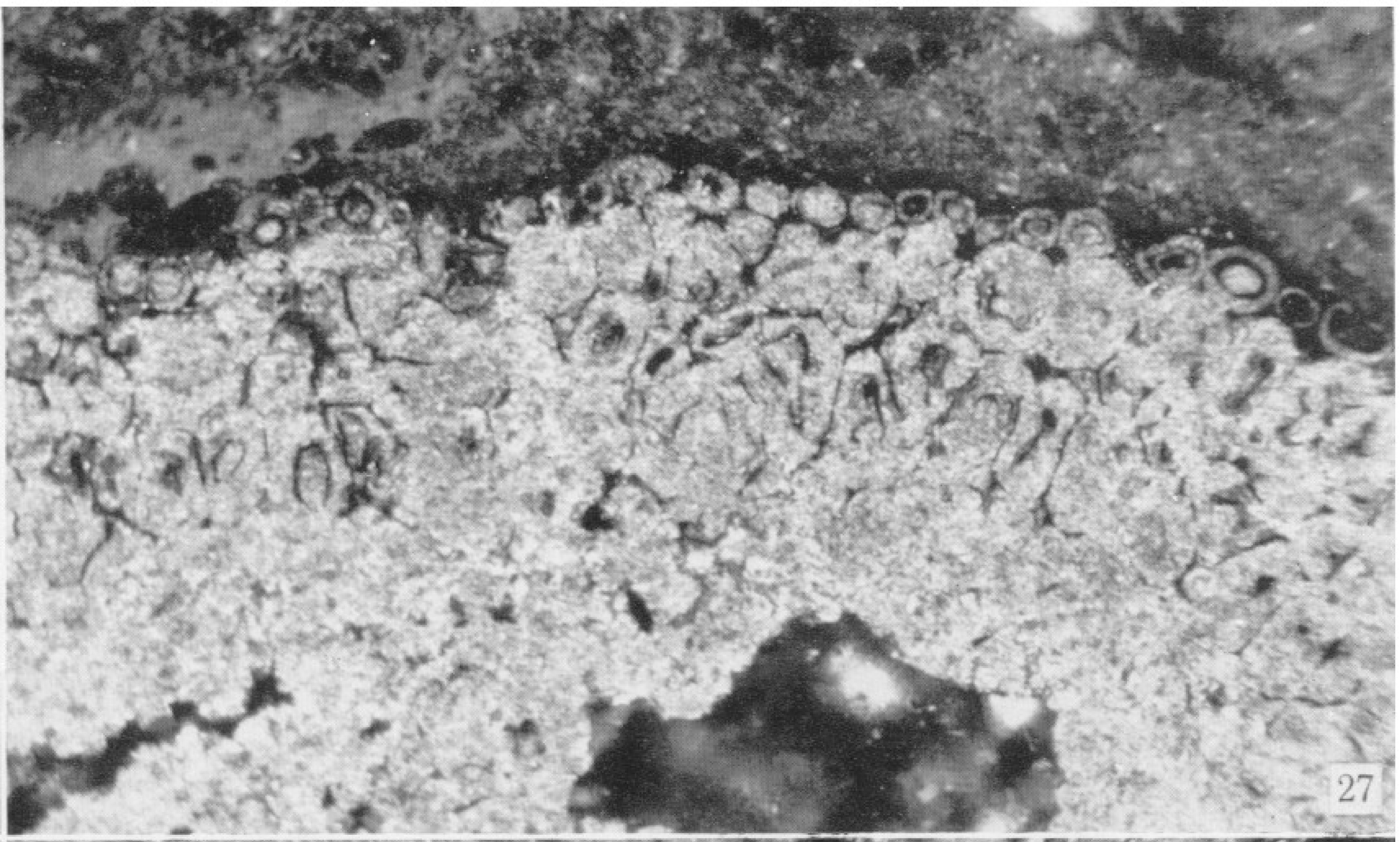
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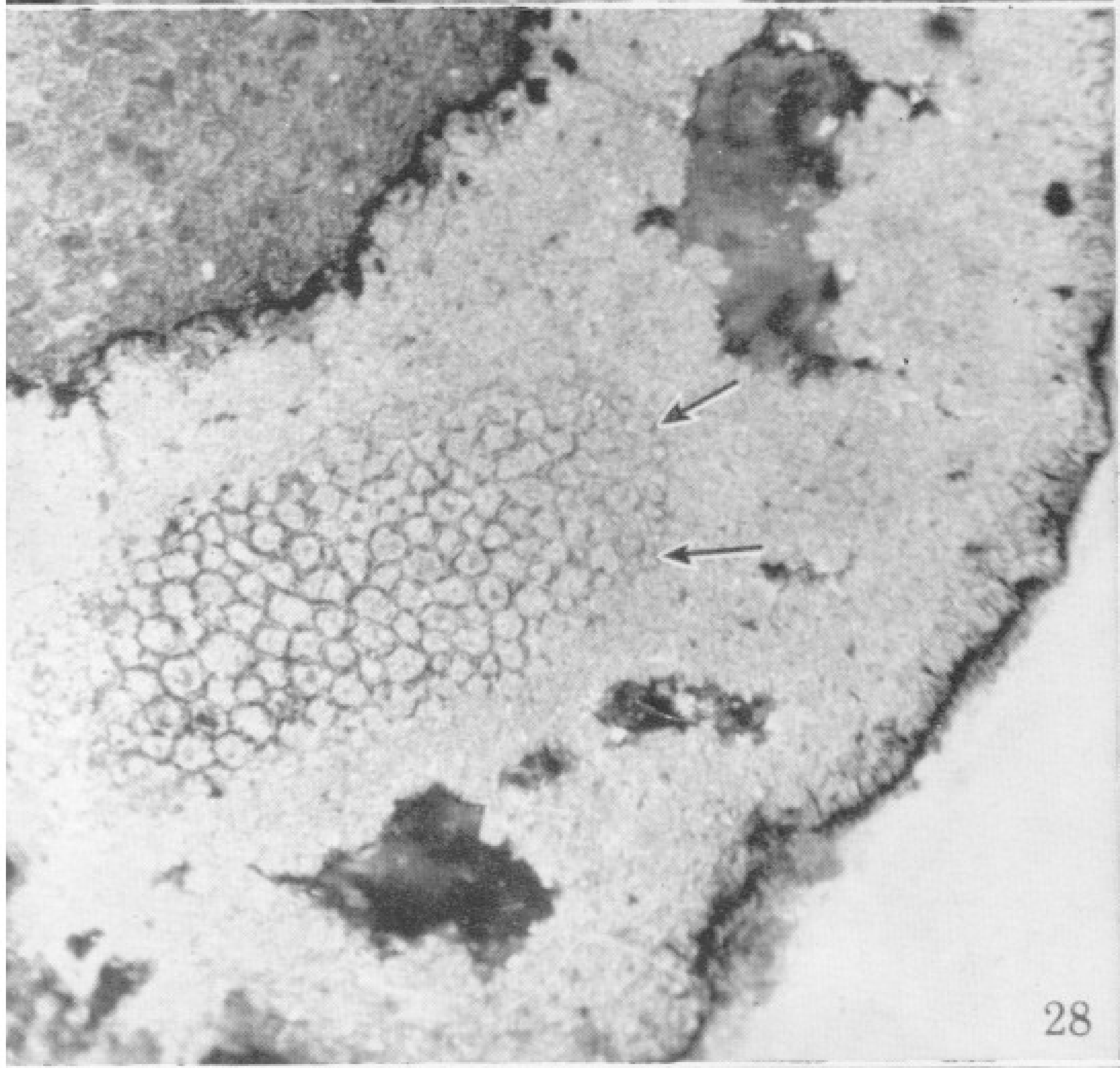
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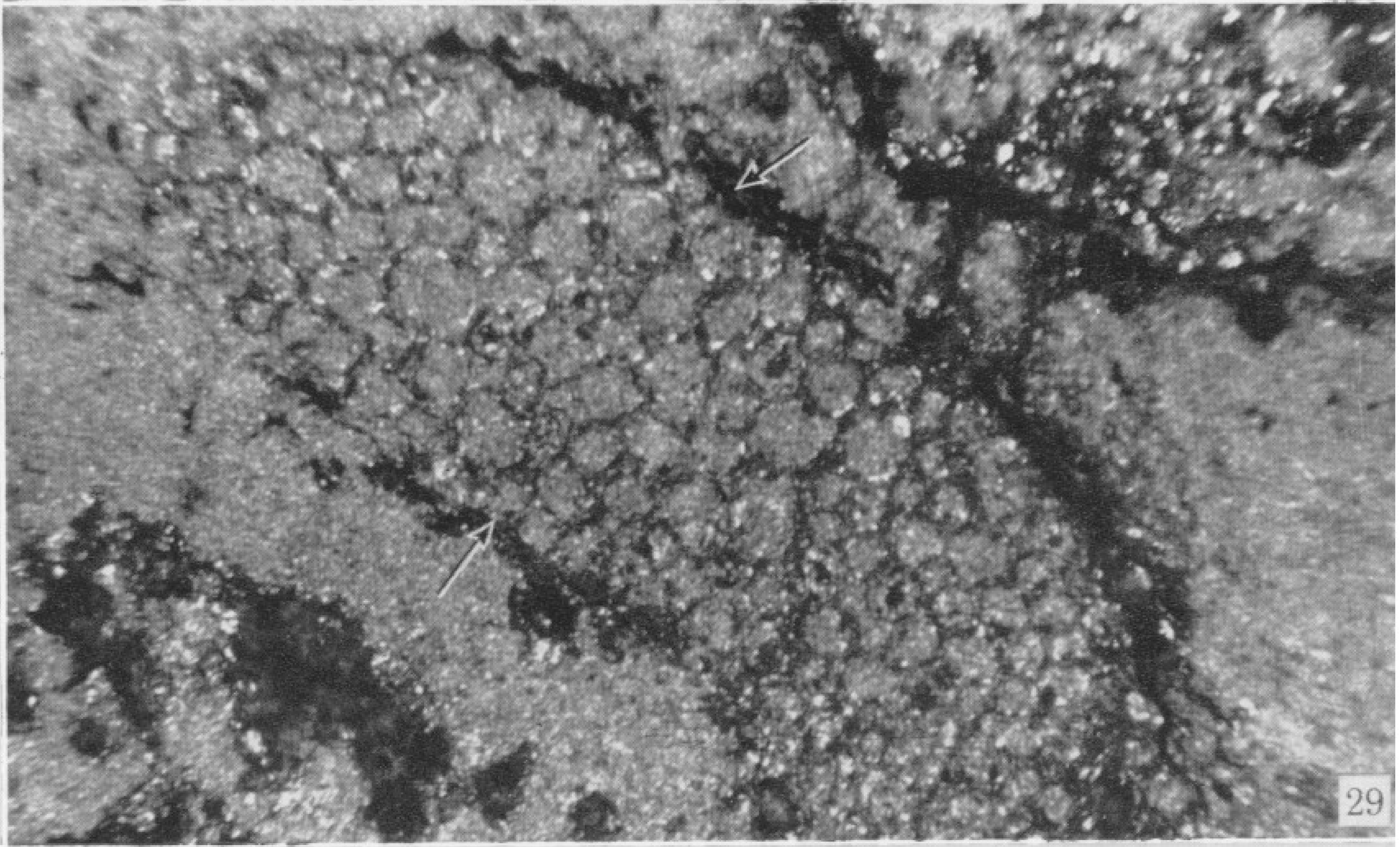
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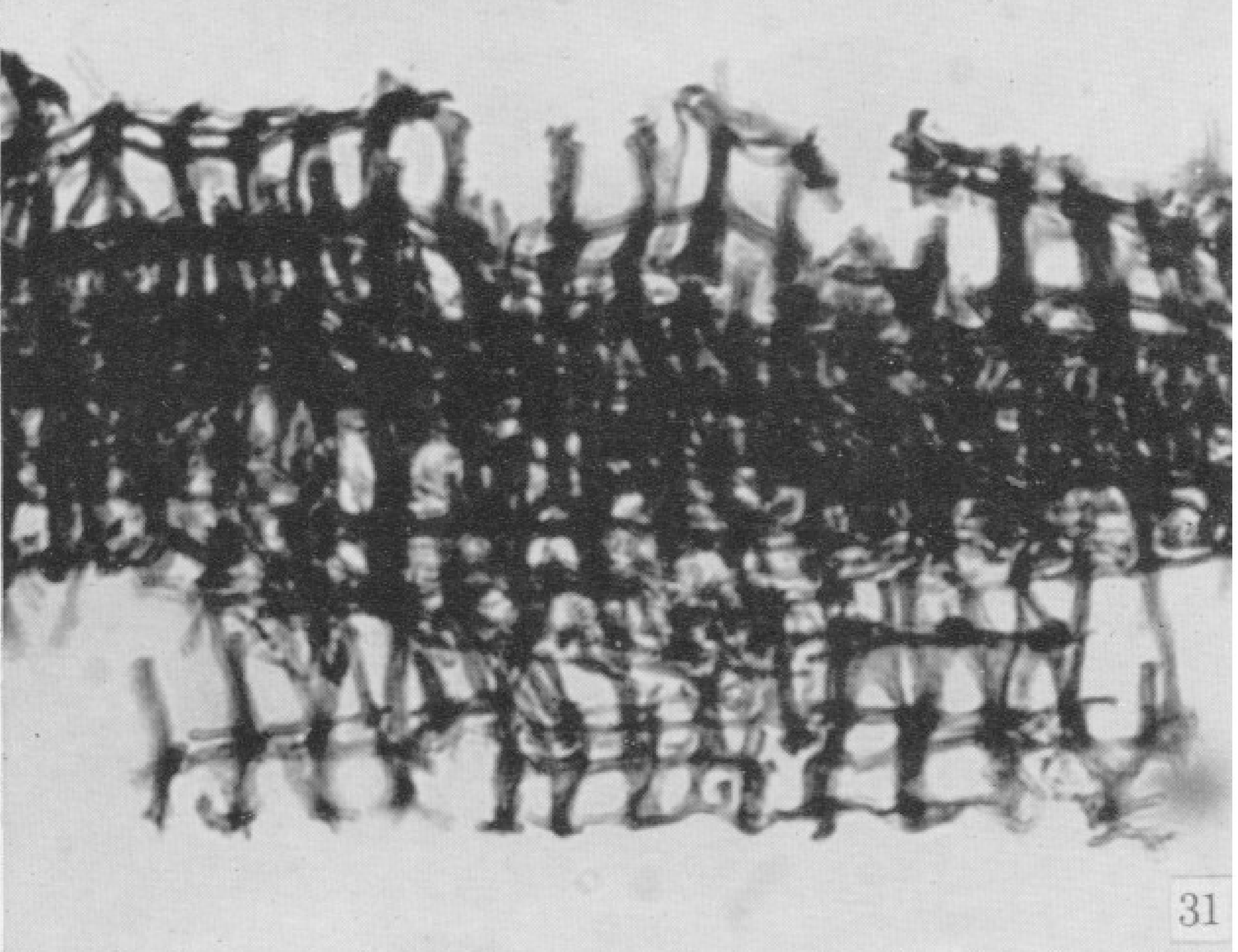
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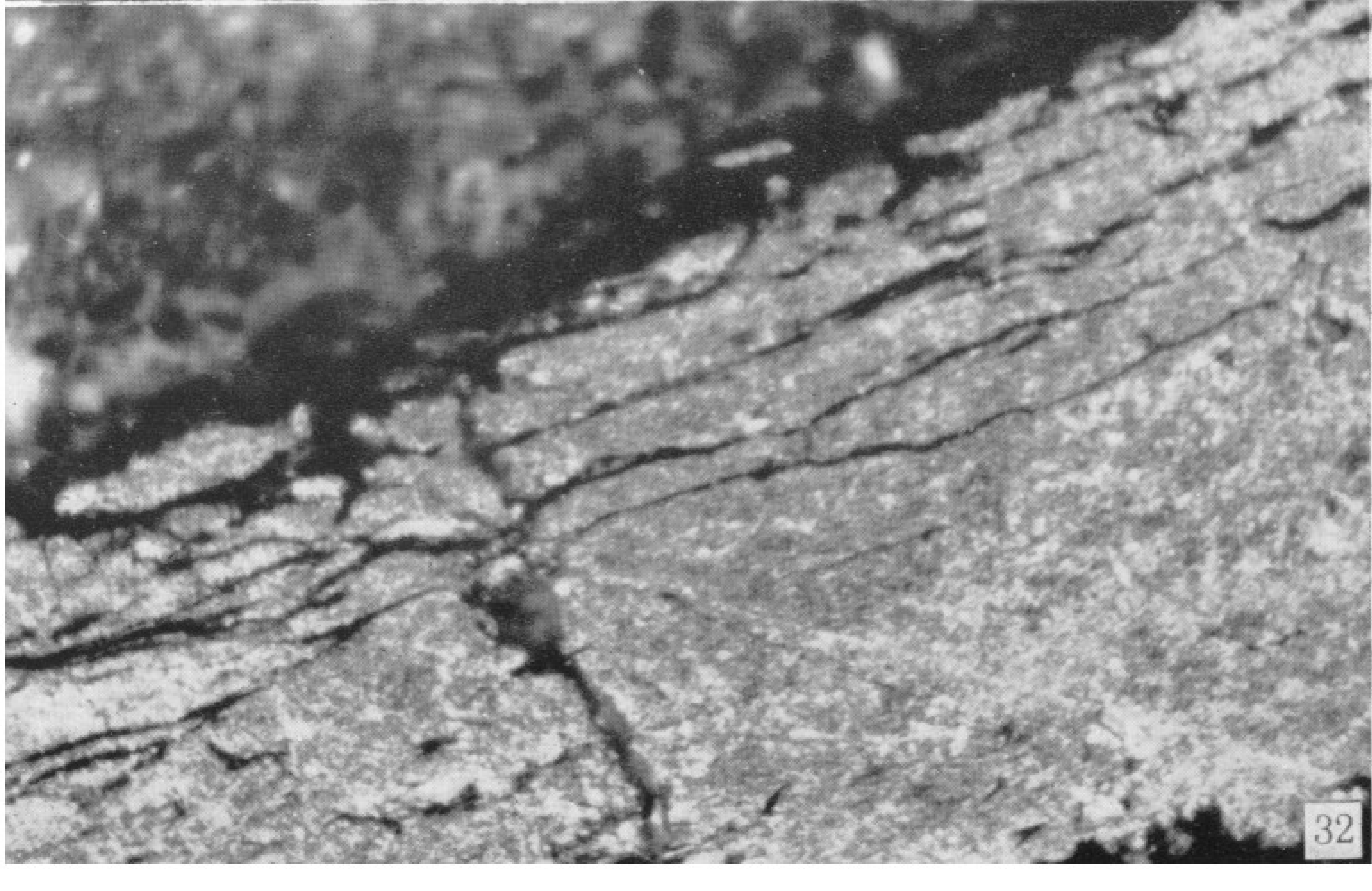
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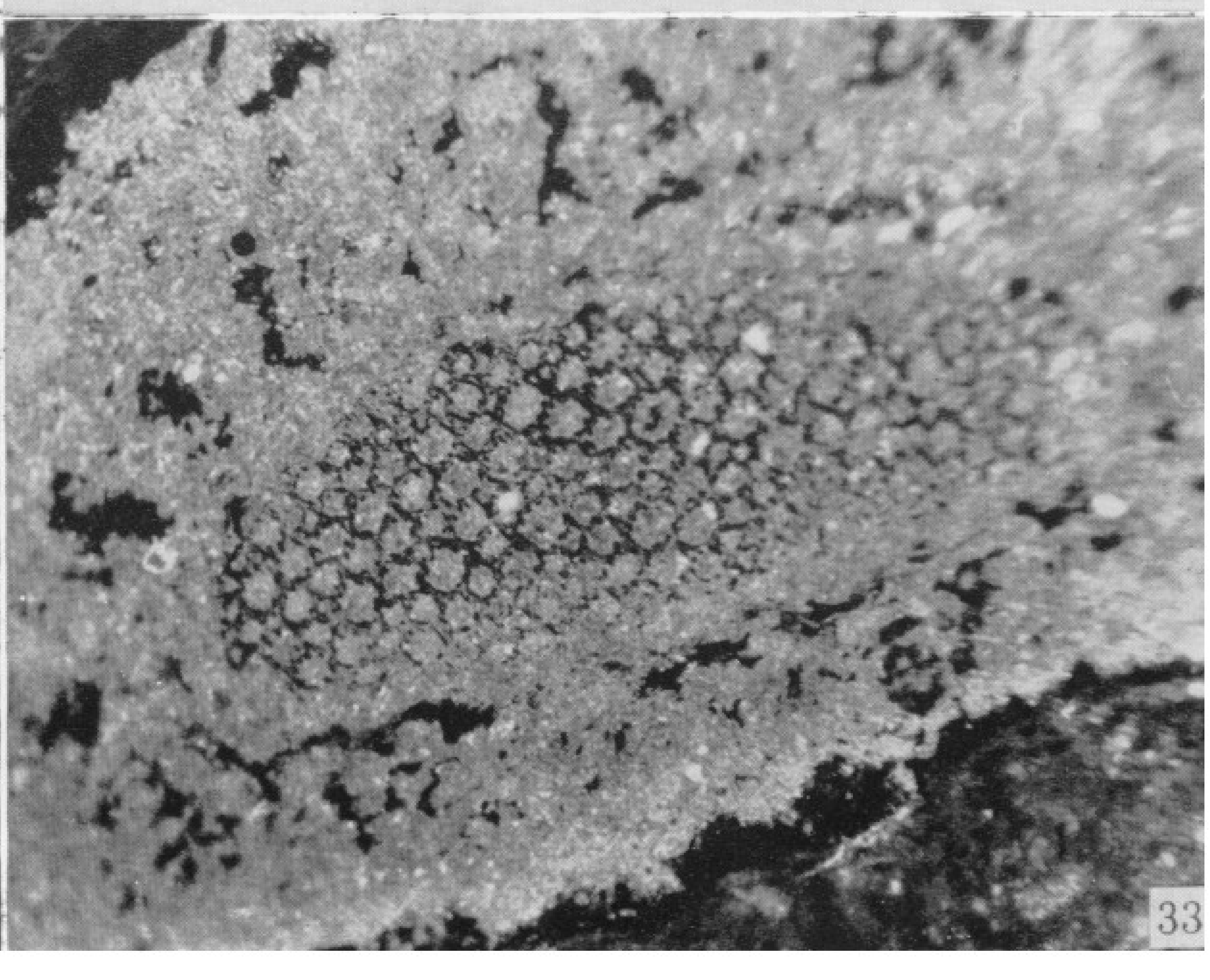
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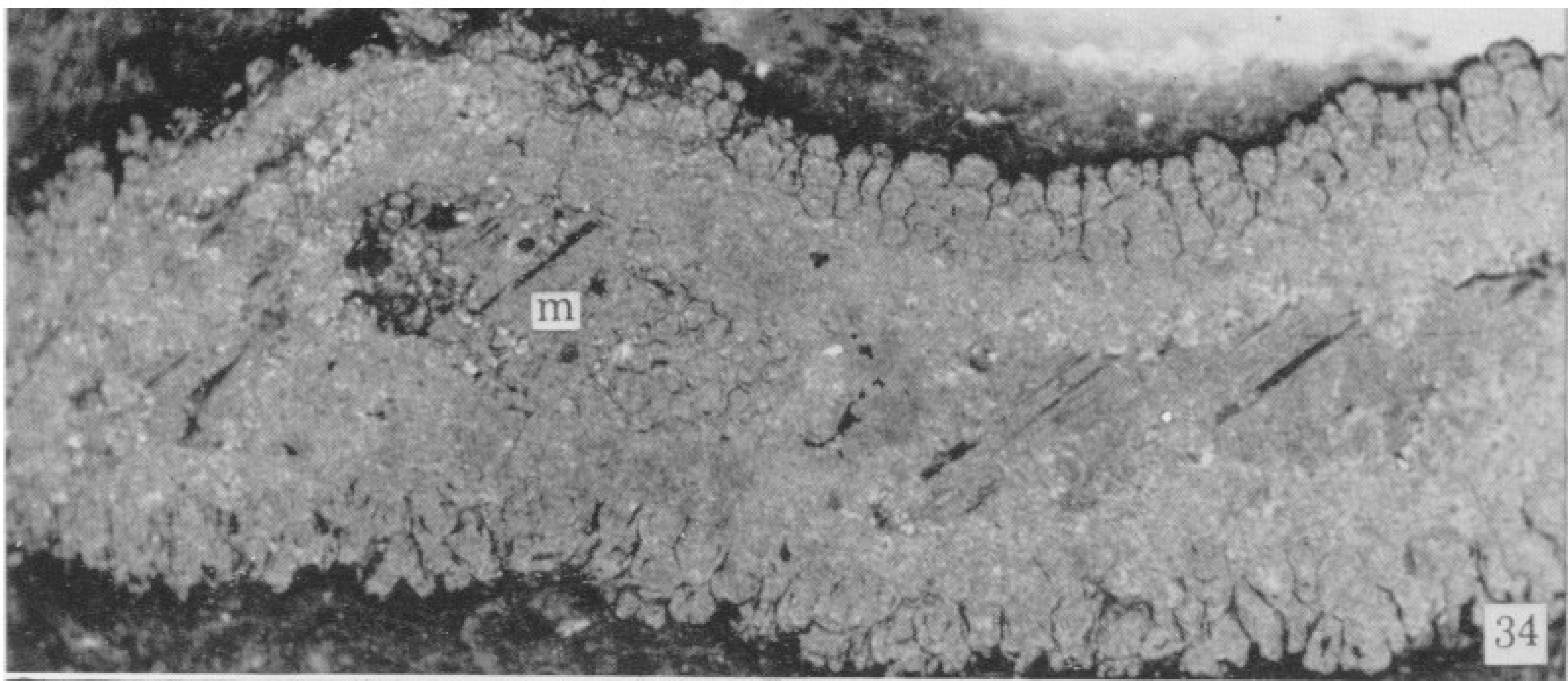

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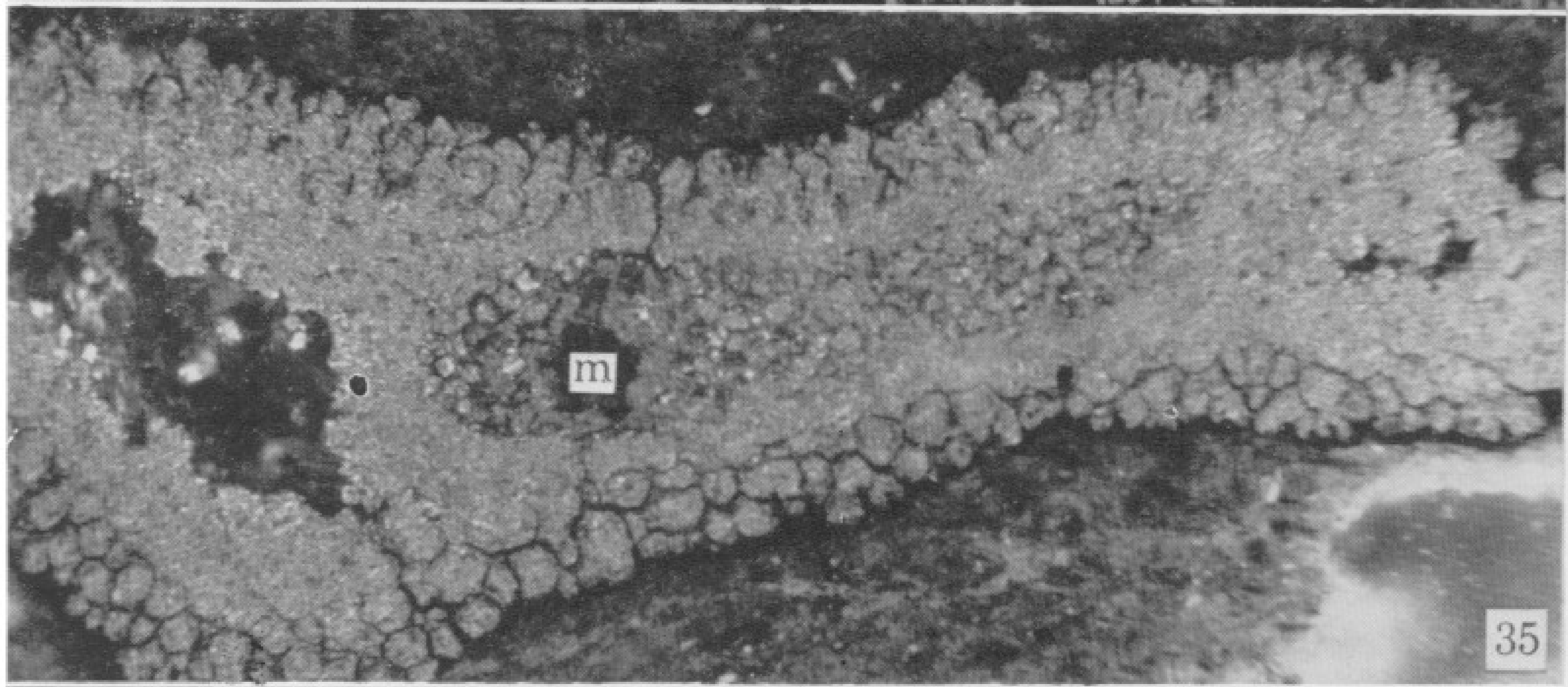

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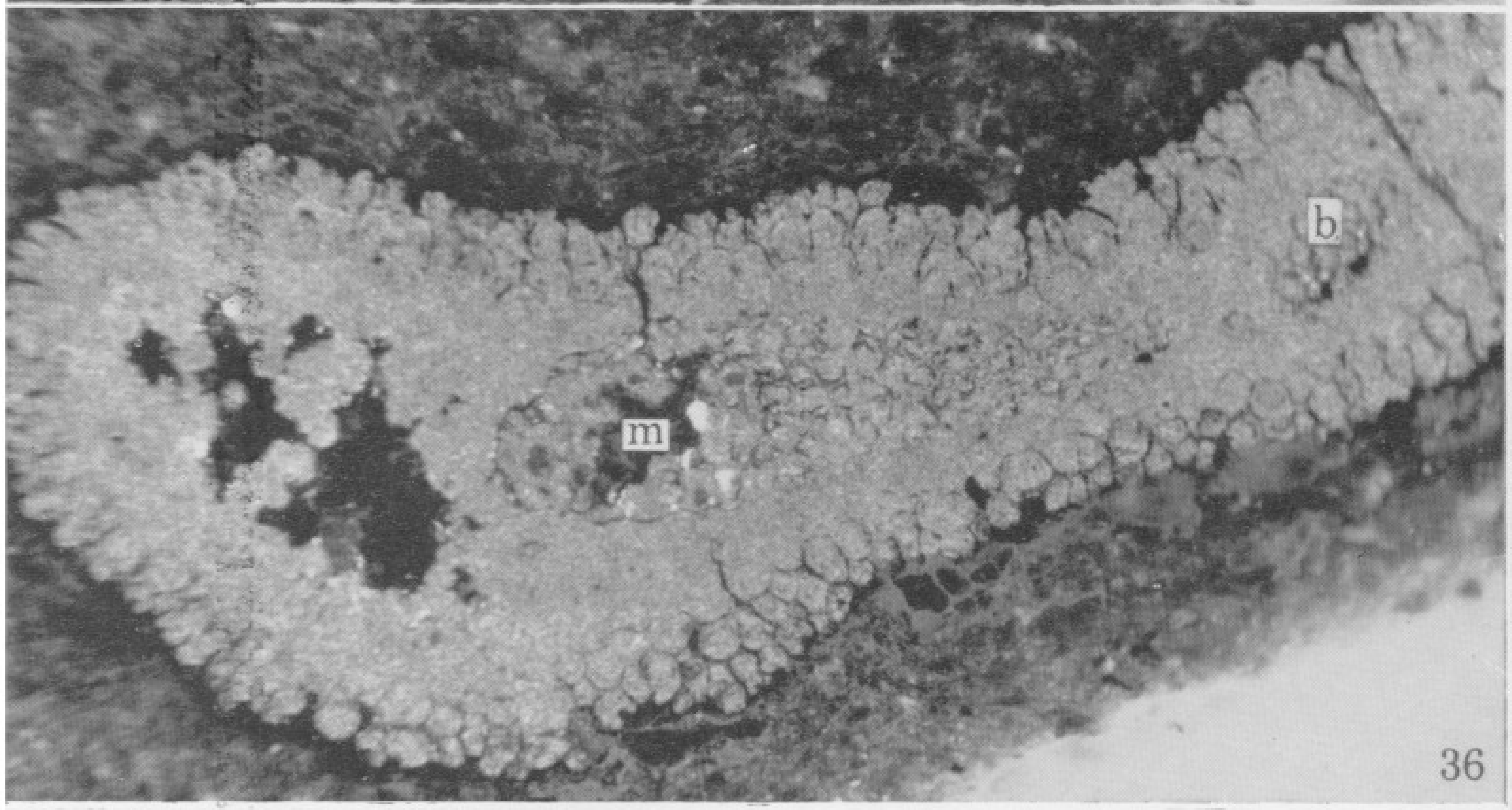

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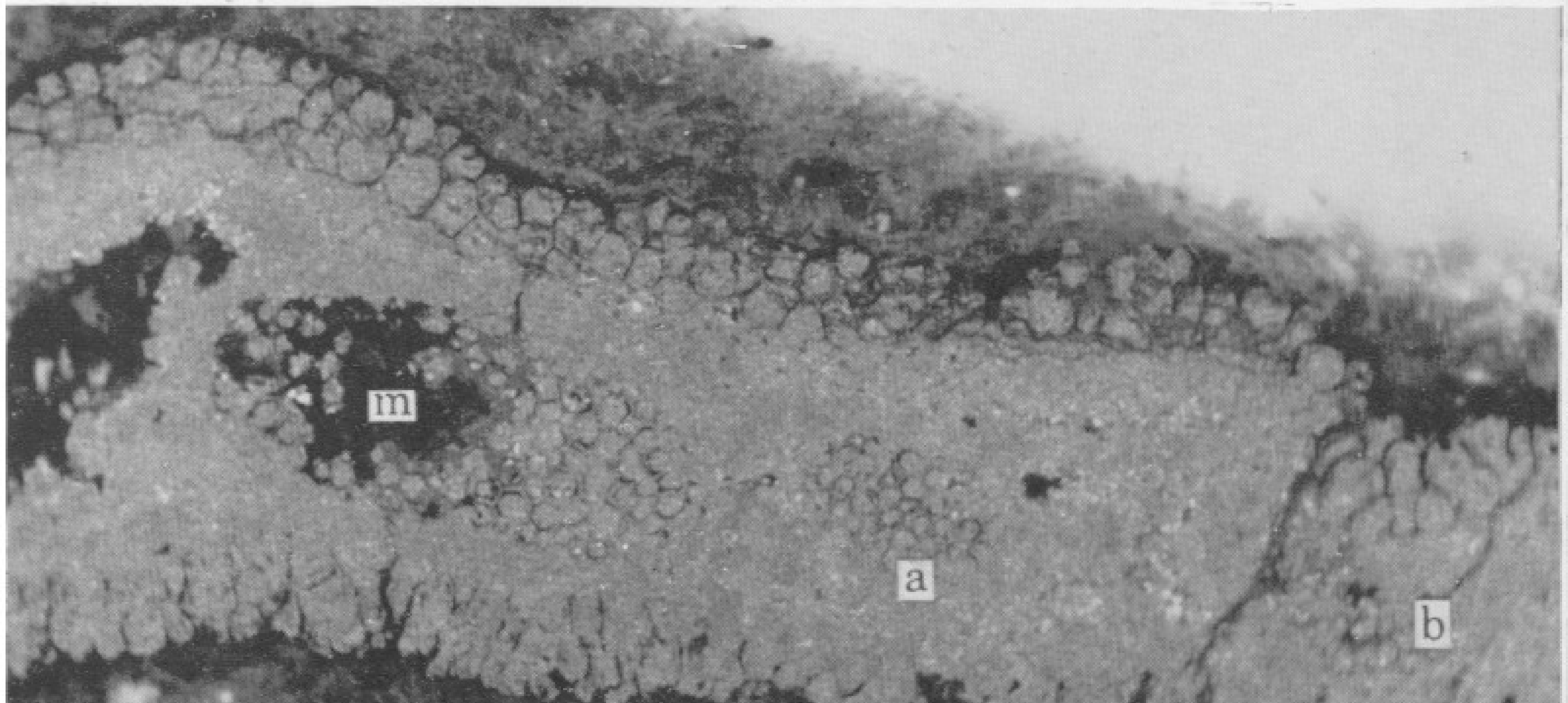

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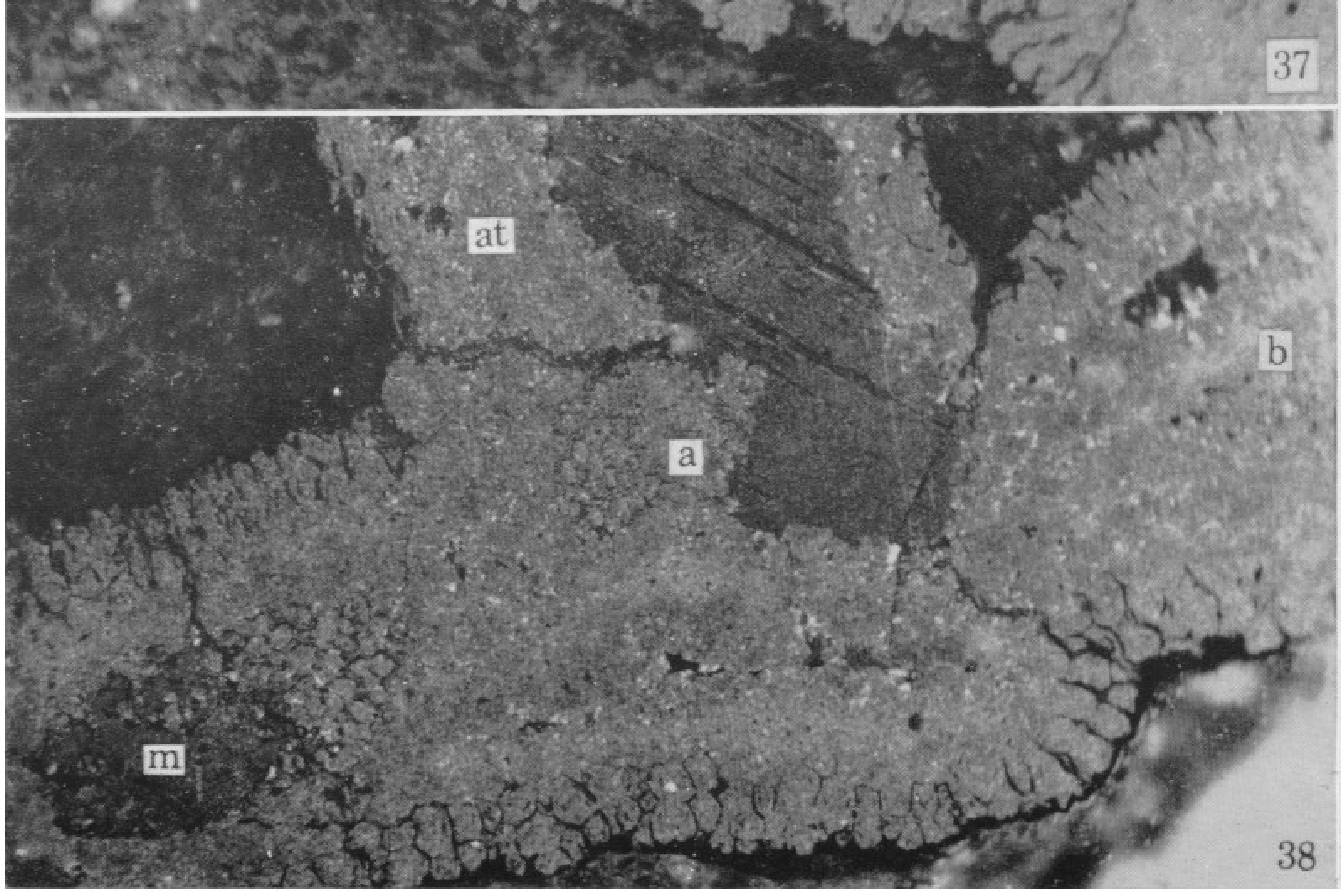

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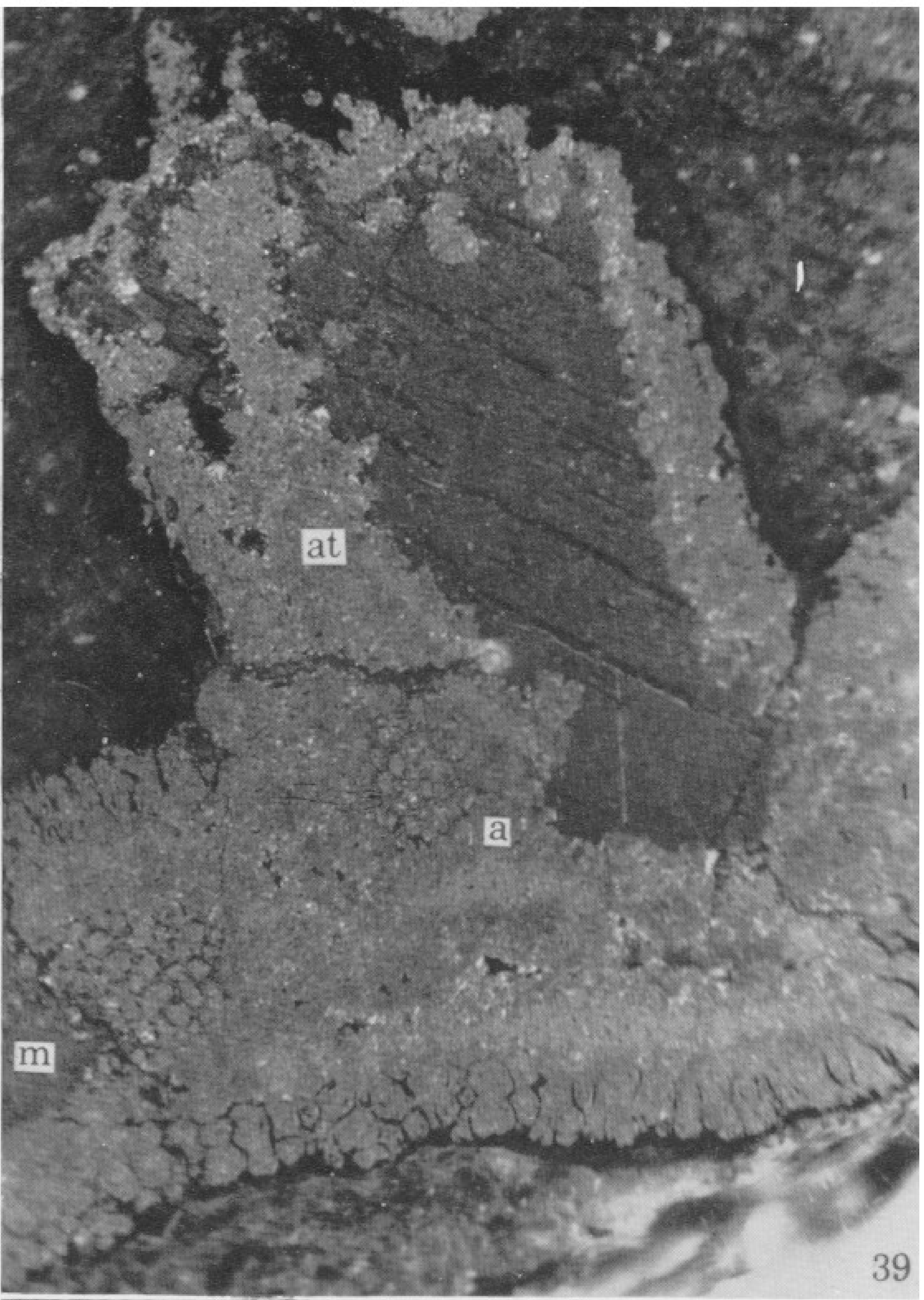

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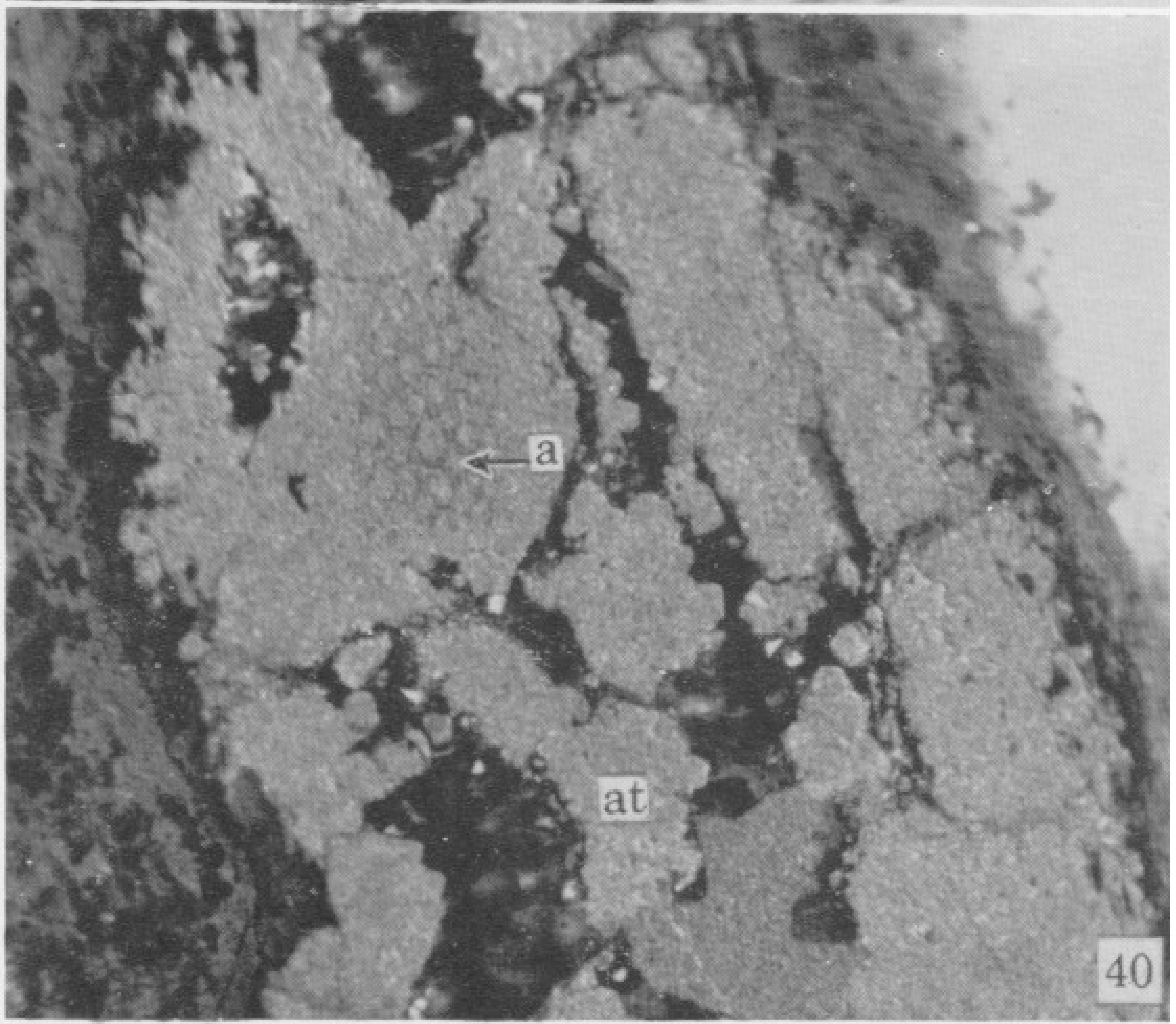

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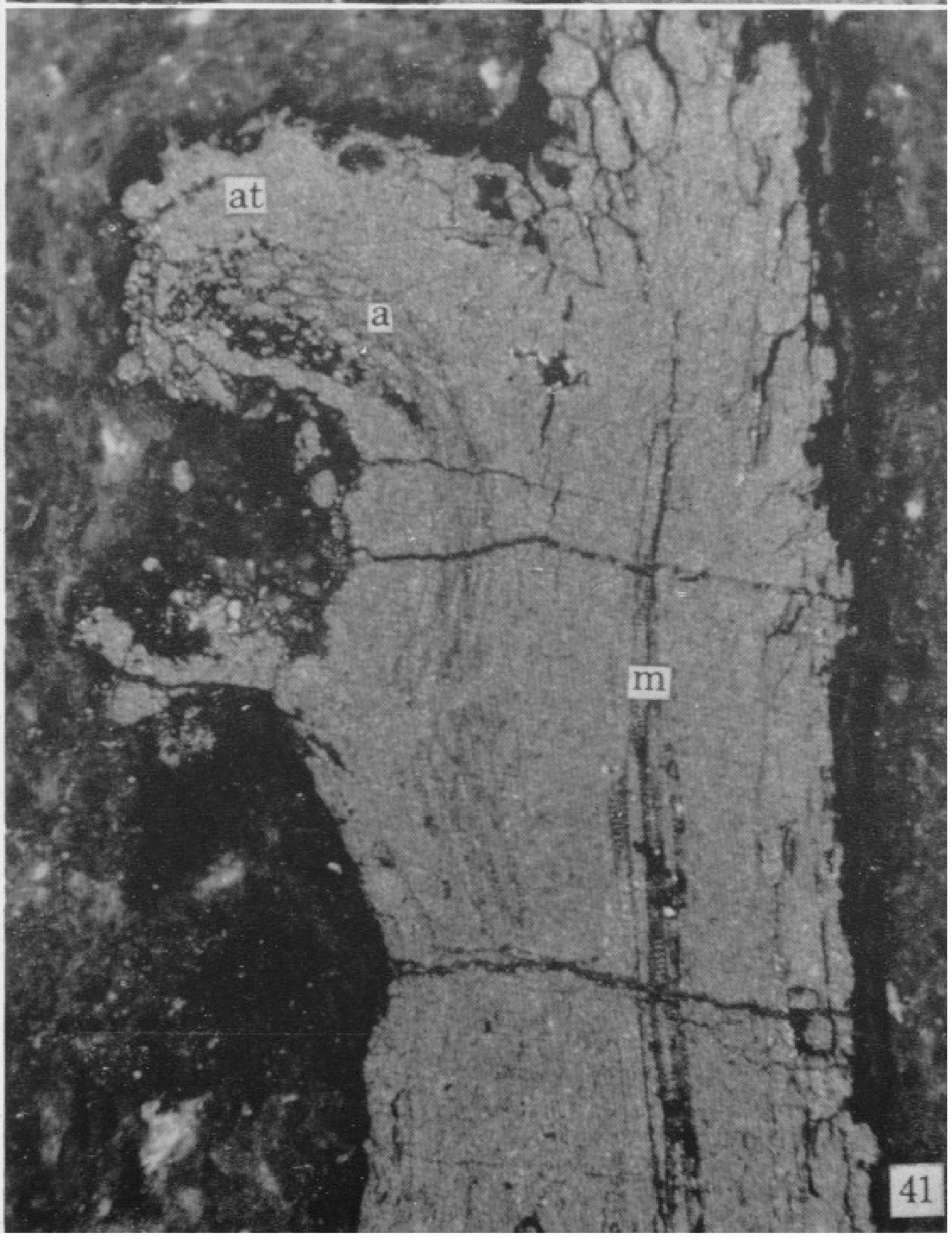

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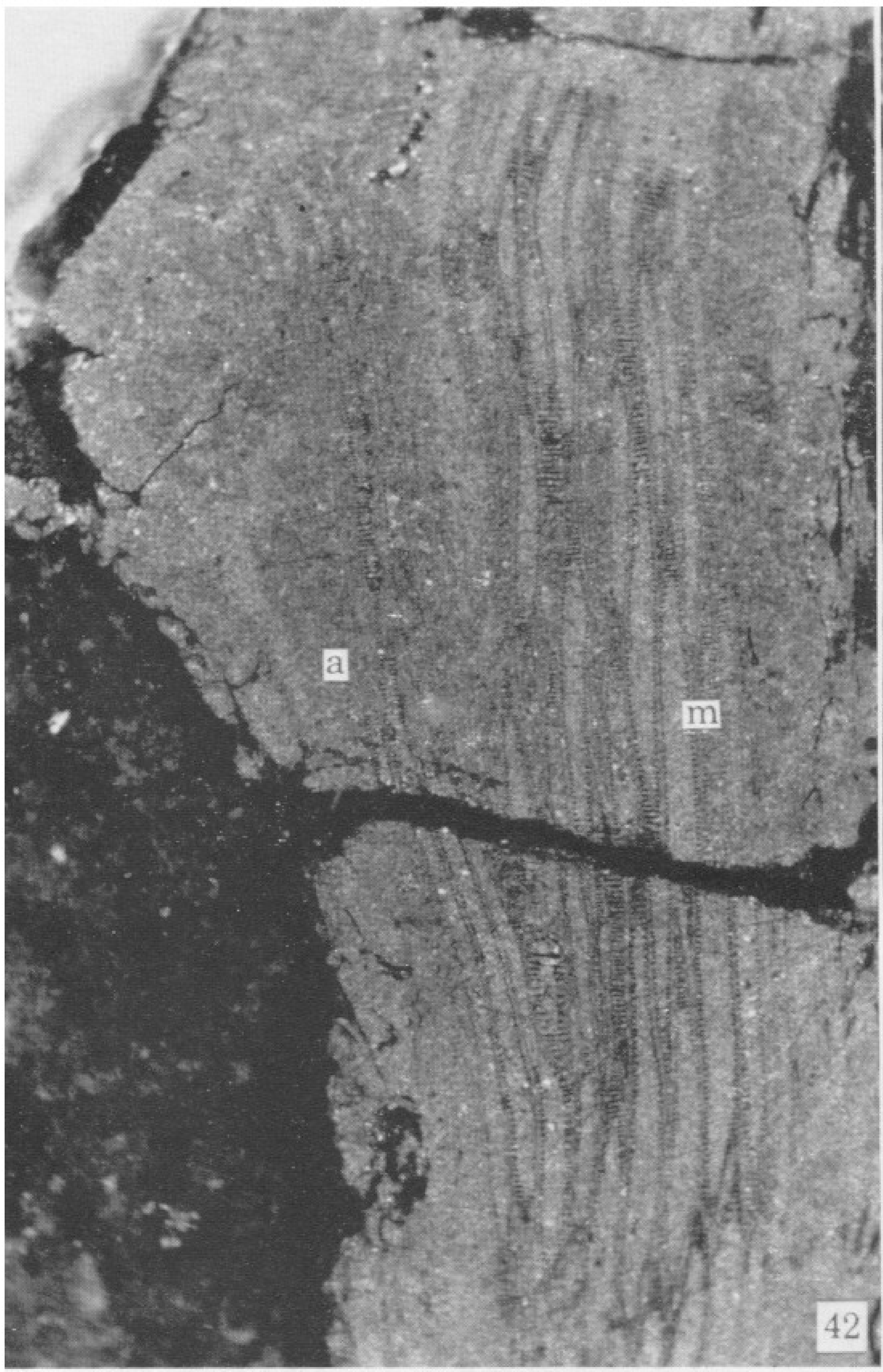

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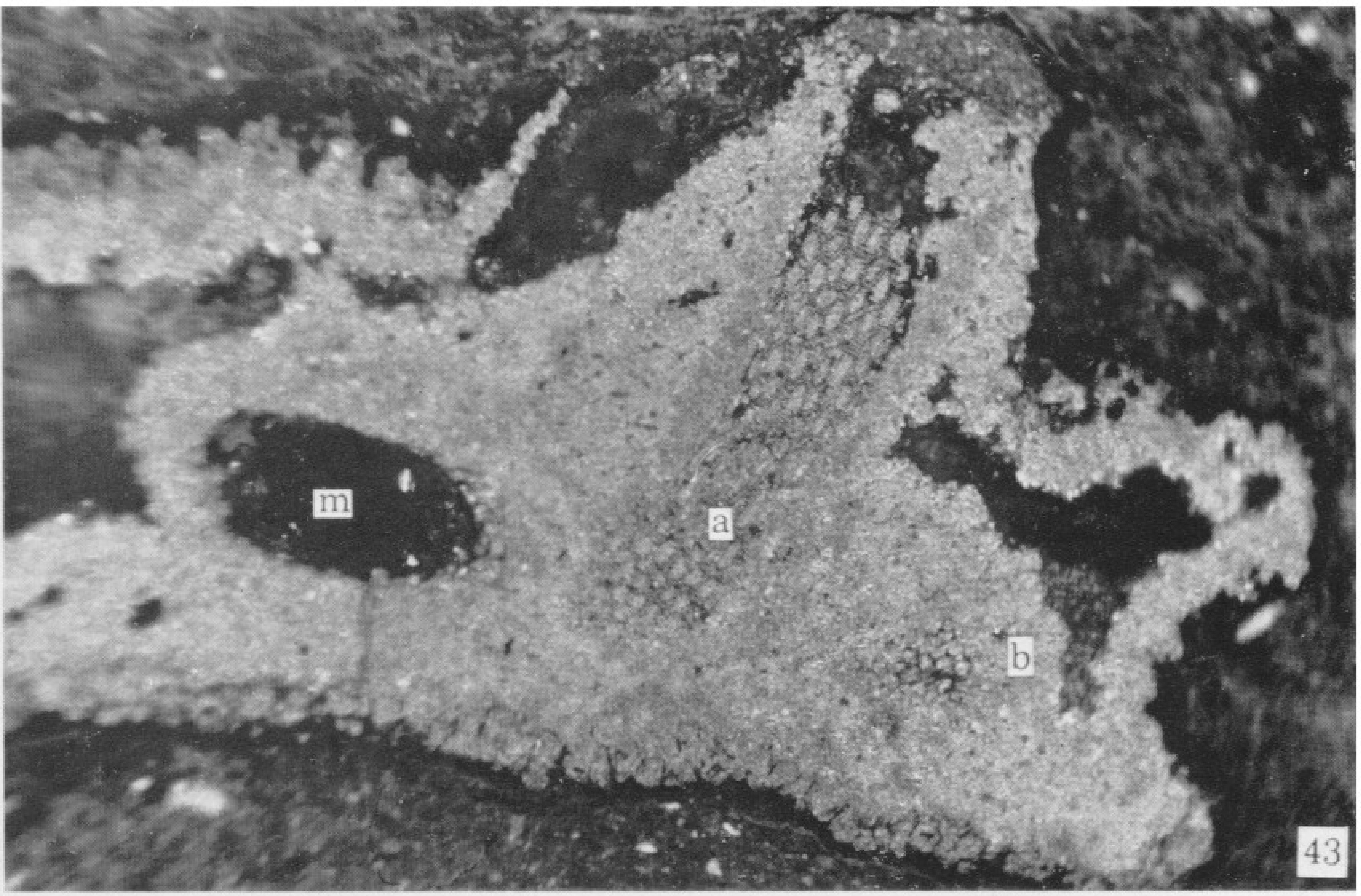

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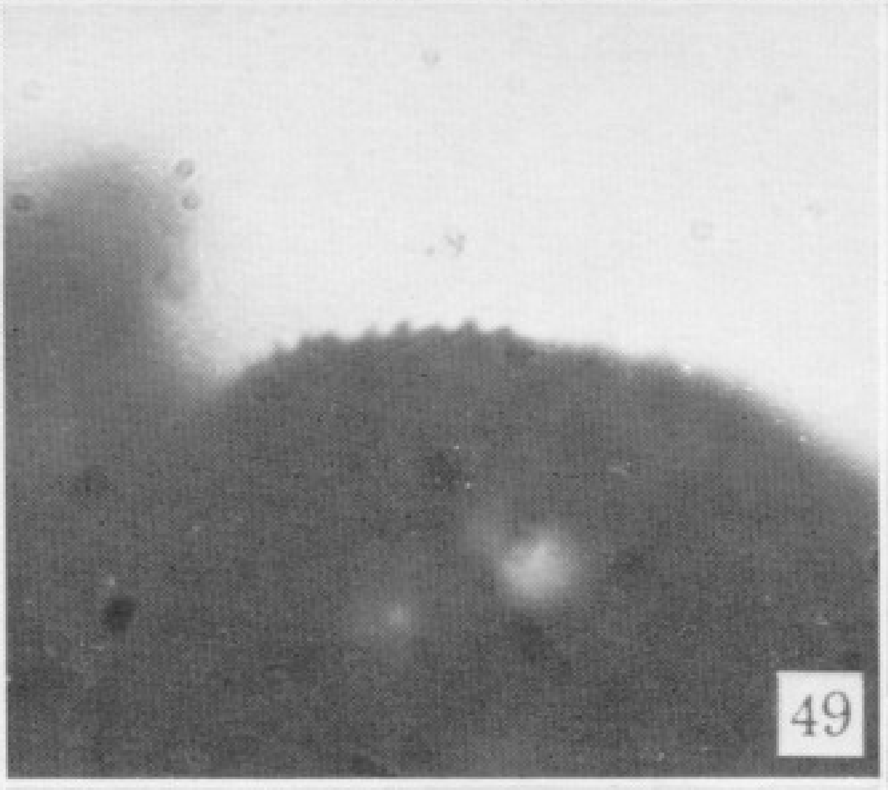

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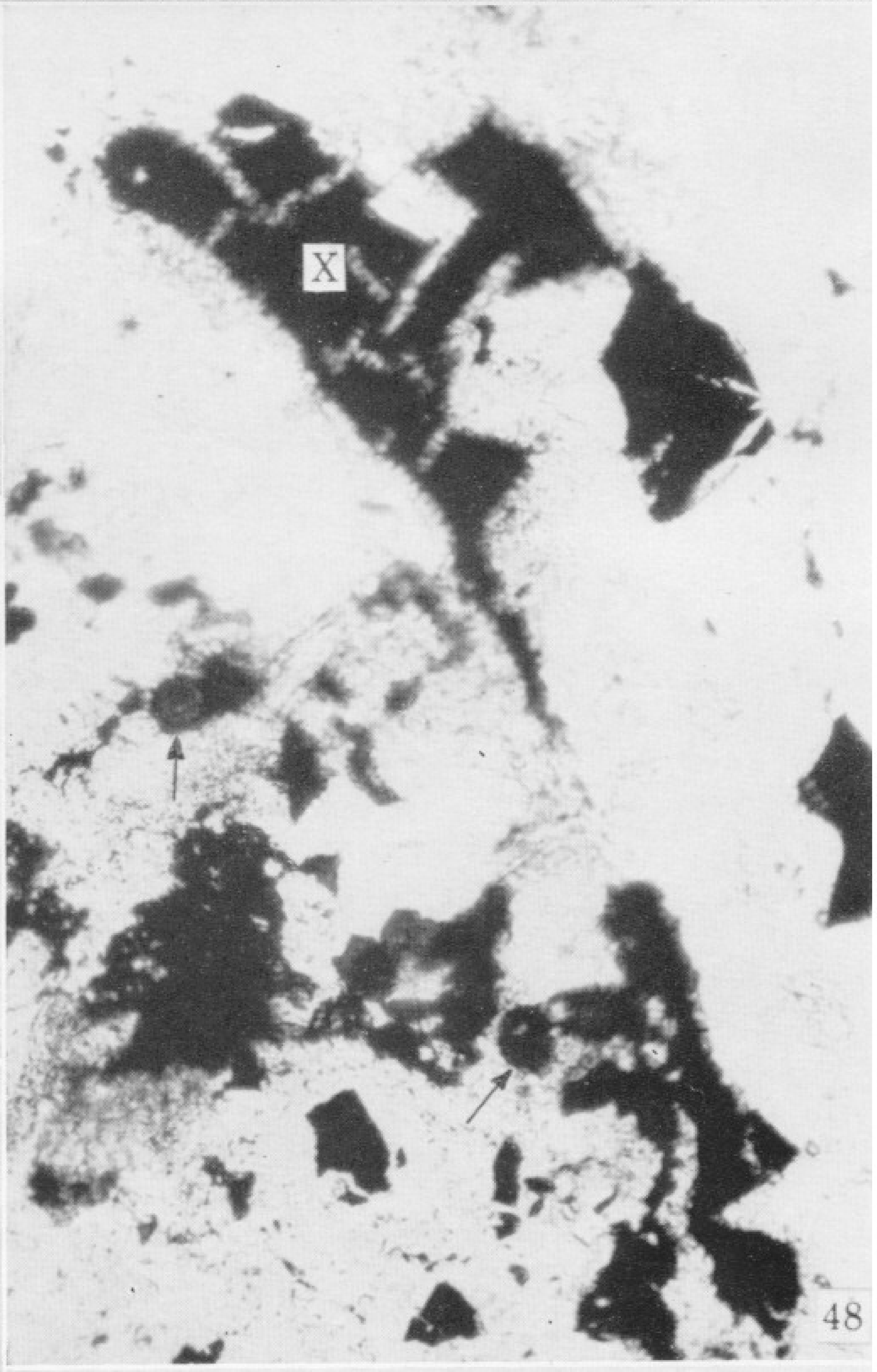

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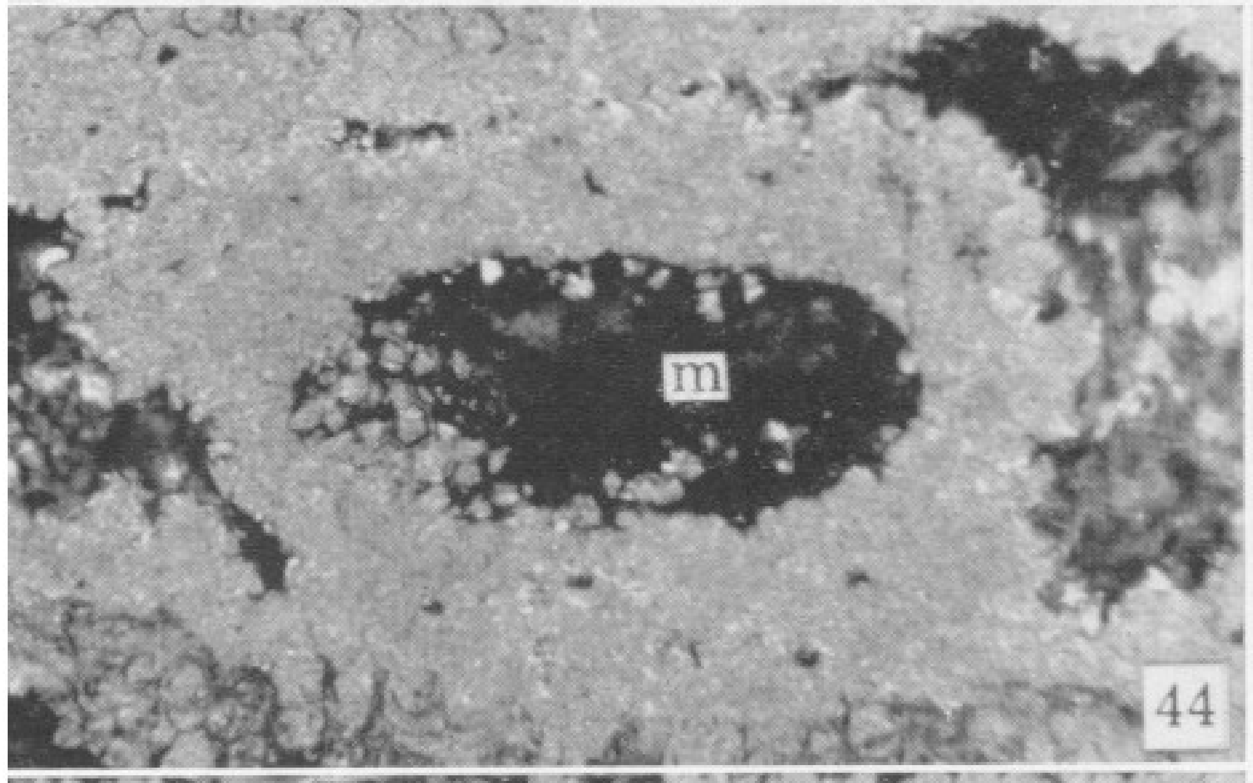

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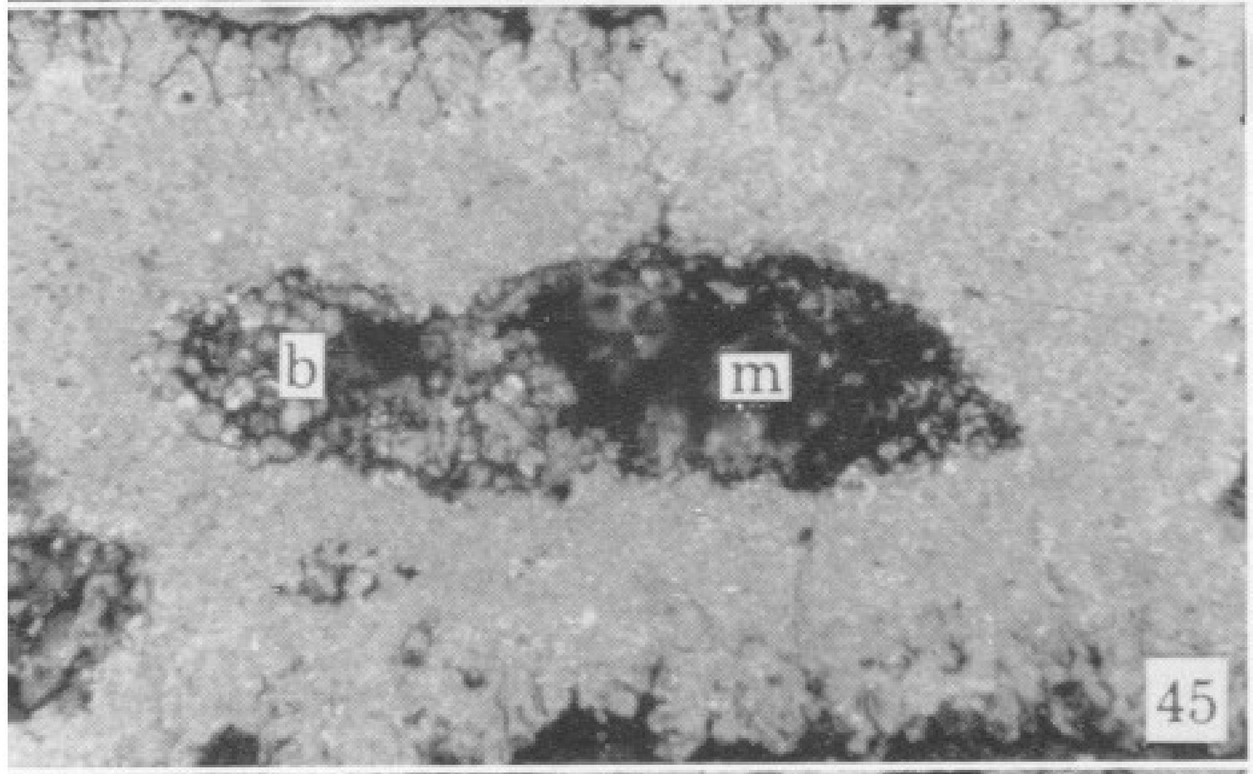

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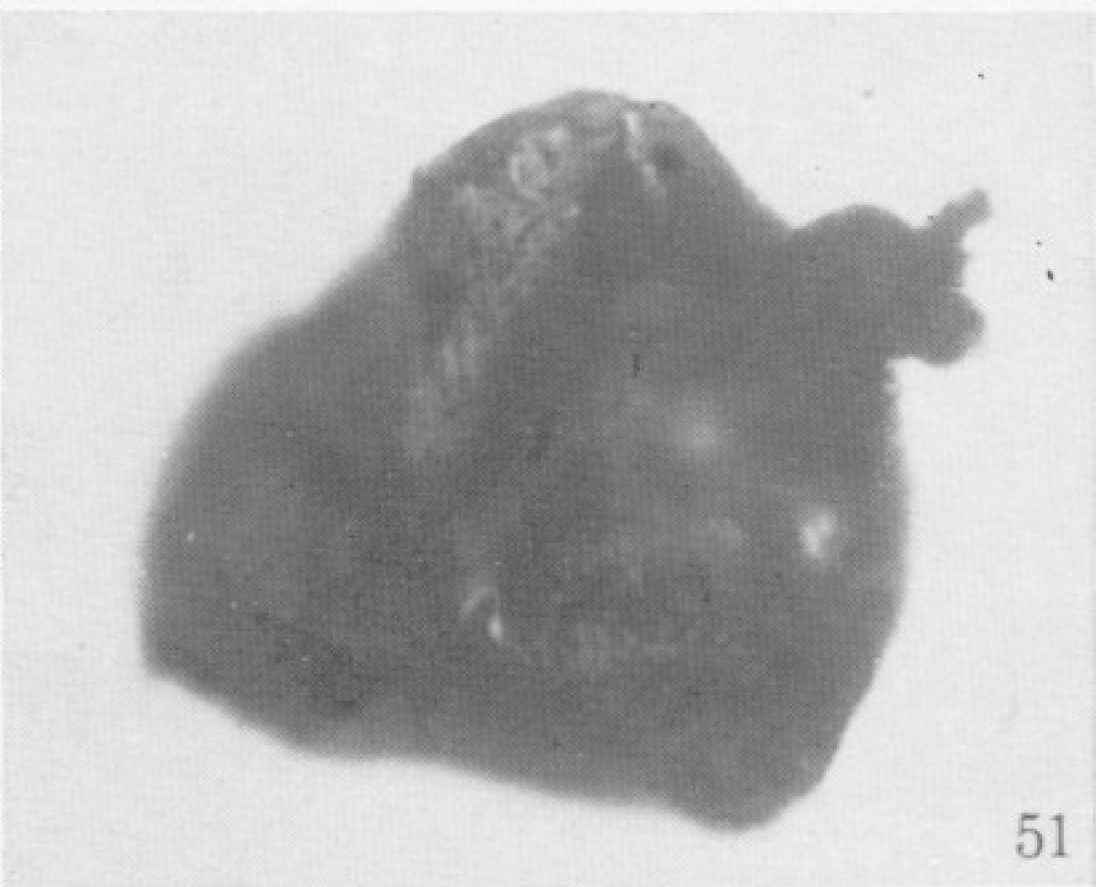

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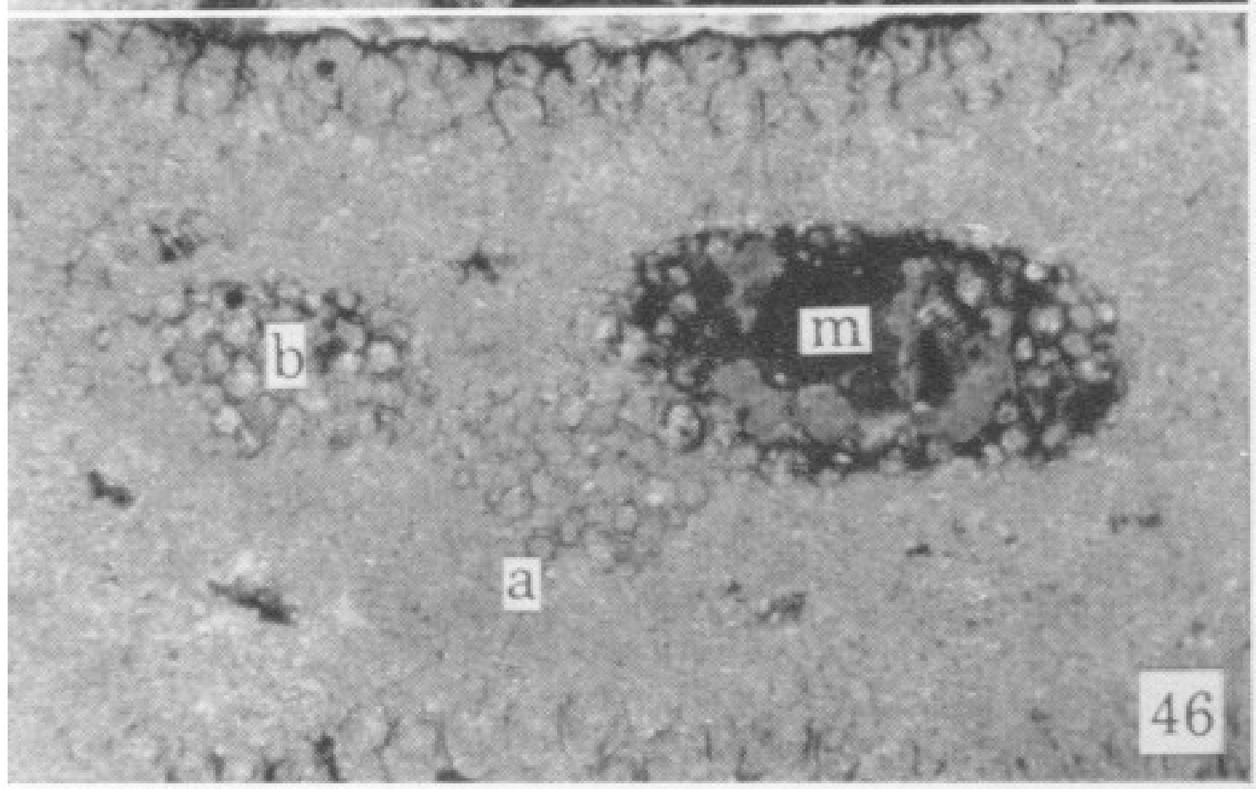

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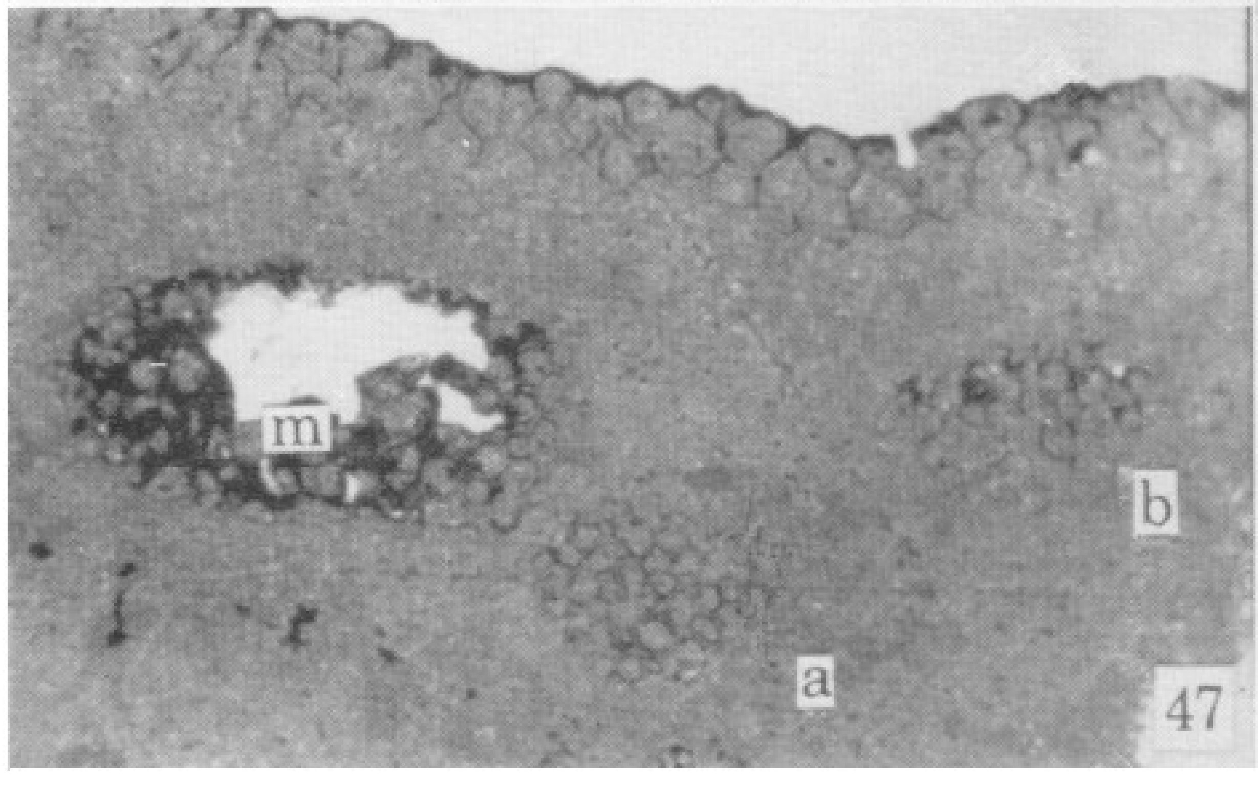

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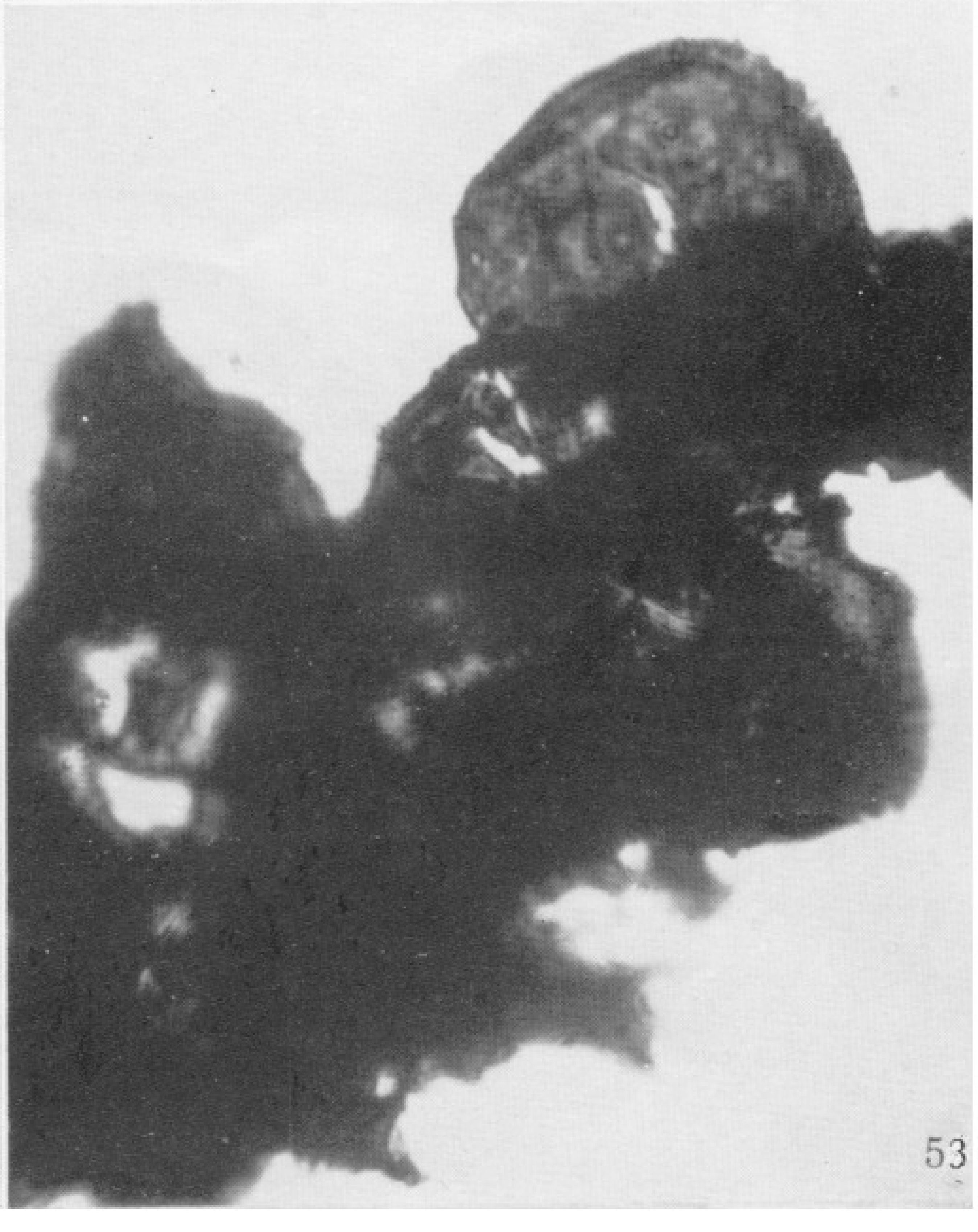

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