# ON THE STRUCTURE OF *BURIADIA HETEROPHYLLA* (FEISTMANTEL) SEWARD & SAHNI AND ITS FRUCTIFICATION*

By D. D. PANT and D. D. NAUTIYAL

*Department of Botany, The University of Allahabad, Allahabad, India*

(*Communicated by T. M. Harris, F.R.S.—Received* 23 *February* 1966)

[Plates 4 to 12]

CONTENTS



The paper gives a detailed account of the morphological and anatomical characters of *Buriadia heterophylla* (Feistmantel) Seward & Sahni based on a fresh examination of the hand specimens in the type collection, located in the Museum of Geological Survey of India, Calcutta, and of new material collected by us from the type locality. Laterally attached solitary anatropous seeds have been discovered in a specimen of the type collection (selected lectotype) and in many duplicates. Maceration of the seed substance shows that they were gymnospermously pollinated by unwinged monocolpate grains. While confirming the gymnospermous character of *Buriadia*, the present study shows that the absence of an organized female cone or any sign of its reduction in the plant indicates that it is either a conifer of an unusual type or a curious plant which is not assignable to any known group of gymnosperms.

## Introduction

Rather few coniferous remains are known in the Palaeozoic beds of Southern Hemisphere and India (see Seward & Sahni 1920; Sahni 1928, 1931; Florin 1938–45, 1940*b*, *c*). In all, seven named species of Lower Gondwana foliage shoots, viz. *Moranocladus oldhami* Seward & Sahni (1920), *Voltzia heterophylla* Seward & Sahni (1920), *Walkomiella australis* Florin (1940*b*), *W. indica* Surange & Singh (1953), *Paranocladus dusenii* Florin (1940*a*), *Paranocladus*?

* An account of this work was presented at the Special Session of the Palaeobotanical Society, Birbal Sahni Institute of Palaeobotany, in December, 1964.

*fallax* Florin (1940*a*) and *Buriadia heterophylla* Seward & Sahni (1920) and Florin (1940*a*) are usually attributed to the Coniferales. However, even these few fossils are incompletely known. According to Shah & Singh (1965) *Moranocladus oldhami* is only an *Araucarites*, as Zeiller (1902) originally called it, and it is of Upper Gondwana (Mesozoic) age. The question mark which precedes the name '*Voltzia heterophylla*', given to some fossils of Raniganj stage by Seward & Sahni (1920), indicates their dubious identification. Neither the fine structure of the above two fossils nor that of *Paranocladus? fallax* is known. Some details of the cuticular structure of the remaining plants have been investigated. Reproductive parts are, so far, known only in *Walkomiella indica*. One of its fertile fragments figured by Surange & Singh (1953) shows among its leaves a single seed attached near the apex. The species is otherwise known only from a few bits of shoots obtained by bulk maceration of coal. The mode of branching of the shoots of this plant and its male fructification are unknown. Numerous compressions of *Walkomiella australis*, *Paranocladus dusenii* and *Buriadia heterophylla* have been reported but their reproductive parts are altogether unknown. Accordingly, when we found a large number of well preserved compressions of *Buriadia* from the type locality and some of these turned out to be fertile, we decided to make a detailed study of their structure and to compare it with that of the shoots in the type material. The results of this investigation, which include a description of a number of previously unknown characters of the plant, a report of its newly found seeds and a discussion of its affinities in the light of these discoveries, are embodied in the present paper.

## Material and methods

The present account of *Buriadia heterophylla* is based on a study of numerous hand specimens collected by us over the last several years from Buriadih, the type locality in the Giridih coalfield. In addition, we have also re-examined Feistmantel's type material located in the collections of the Geological Survey of India, Calcutta. The remains of *Buriadia*, in the type collection as well as in our specimens, are in a dark coloured sandy siliceous shale. The hand specimens are littered with compressed shoots and contain no other fossils except stray fragments of *Glossopteris* and *Noeggerathiopsis*. External features of the plant were studied in strong unilateral incident light. Transfers of shoots were prepared by the use of hydrogen fluoride. Cuticles of the stems, leaves and seeds from the new hand specimens as well as from the type material were prepared by macerating their substance in Schulze's fluid. They were subsequently mounted in glycerine jelly for microscopic examination. Treatment of the rock matrix with hydrogen fluoride occasionally yields brownish fragments of the plant and these were mounted in Canada balsam to make them translucent. Microtome sections of the leaves were prepared by embedding them in colloidin or paraffin. The internal structure of the stem has been studied partly by examining maceration residues of its carbonaceous substance and partly by splitting it with needles and observing the small chips so obtained under the microscope in strong incident light. It appears that the compressed axes of the plant are often partially mineralized and small chips of their semi-petrified wood, therefore, yield valuable information about its fine structure.

FIGURE 1. Compressions of foliage shoots. Specimen 710. (Magn. × 3.)

FIGURE 2. A thicker axis showing branch scars. Specimen 708. (Magn. × 5.)

(*Facing p.* 28)


FIGURE 3. Twice branched longitudinally ribbed fragment of a shoot. The ovoid scars seen on the leafless shoot of the first order and also on one of its leafy branches are brownish spots on the rock. Specimen 694. (Magn. × 1·5.)

FIGURE 4. Branching foliage shoots, one of them with an attached seed. A thick leafless axis (towards the left) and a detached seed are also seen. Specimen 717. (Magn. × 0·8).

FIGURE 5. Portion of a branched shoot in figure 4, more magnified to show the attached seed (*s*), and the apical bud. A detached seed (*ds*) is also seen. (Magn. × 3.)

All newly figured duplicate hand specimens and slides form part of the Divya Darshan Pant Collection at present located in the Palaeobotany Section of the Department of Botany, Allahabad University (India).

## Description

### External morphology

*Stem*

Figures 1 to 9, plates 4 to 6; figures 72 to 78, plate 12; and figures 79, 80, as also the various figures of shoots of *Buriadia* given earlier by Feistmantel (1879), Seward & Sahni (1920) and Florin (1940*a*) clearly depict the gross features of the plant. The irregularly ramified shoots of *Buriadia* form a spreading monopodial system. As a rule the branches are alternate but a few are almost opposite (see figure 9, plate 6). The ultimate branches arise at short intervals but the penultimate axes are less crowded. The branches of various orders arise at varied angles. The thickest stems are up to 27mm wide and may bear raised and rounded scars of fallen branches (see figure 2, plate 4; figure 80 *A*). The leaves of the thicker stems apparently fell off. They show attached leaves rarely and even the leaf bases are obscure. The surface of some of the thickest leafless shoots shows longitudinal or obliquely running linear marks which may occasionally anastomose to form a network of very narrow and much elongated rhomboidal meshes. Some of them run to a leaf base and as Seward & Sahni suggested they may be foliar traces but we are uncertain. The ultimate and penultimate branches are characterized by the presence of more or less crowded and spirally disposed leaves. Apices of ultimate branches often terminate in buds with closely imbricated leaves.

*Leaves*

The leaves of the plant are only slightly spreading. Their form varies and they may be broadly classified into three categories, viz. (i) simple undivided leaves, (ii) bifid leaves, and (iii) multifid cuneate leaves. The simple leaves may be linear or ovate lanceolate, or tapering and acicular. The bifid leaves exhibit a shallow or a deep incision between their two equal or slightly unequal segments (figures 10 to 15, 25, plate 7). The lobes of bifid leaves may occasionally overlap each other by being compressed in a plane which is at right angles to that of their branching (figures 10, 11, 14, 15, plate 4). Some of them do so by twisting. The multifid leaves, which we have seen only in the material of Feistmantel, are cuneate and their segments too may be equally or unequally incised (figure 79 *A*, *B*). All kinds of leaves have broad attachment and the leaf base is invariably decurrent. The apices of the leaves or their segments show all transitions of shape, ranging from an obtusely pointed tip to a narrowly acute apex (figure 10 to 32, plate 7). Multifid leaves and also some leaves of other forms appear dorsi-ventrally flattened and bifacial but other simple and bifid leaves show a prominent ridge running longitudinally up to their tips and this divides the surface of such leaves into three faces. Under similar lighting one of the faces in bifacial leaves as well as in trifacial ones shows outlines of rectangular cells. Their remaining face or faces have numerous raised papillae (figure 36, plate 8). The interfacial ridges also show papillate projections. Generally, the two margins of bifacial leaves and the two edges bounding the non-papillate faces of the trifacial leaves also are normally


FIGURE 79. *Buriadia heterophylla*. *A*. Selected lectotype showing a branched shoot. The branches show two attached seeds (*s*), simple, bifid and multifid leaves. *B*. Another fragment of a shoot showing multifid leaves. *C*. Shoot with simple and bifid leaves. A seed is also seen near the apex. *D*. A shoot with two opposite branches. The central thicker axis shows an attached seed. The surface of the thicker axis is marked with longitudinal lines, some of which enter a side branch (on the left). *E*. Marginal hairs of a leaf (see also figure 21, plate 7). *A*, *B*, G.S.I. specimen 5043, *C*, specimen 717, *D*, specimen 701; *E*, slide 757 (*A*, *B*, *D*, magn. ×1·5; *E*, ×75).

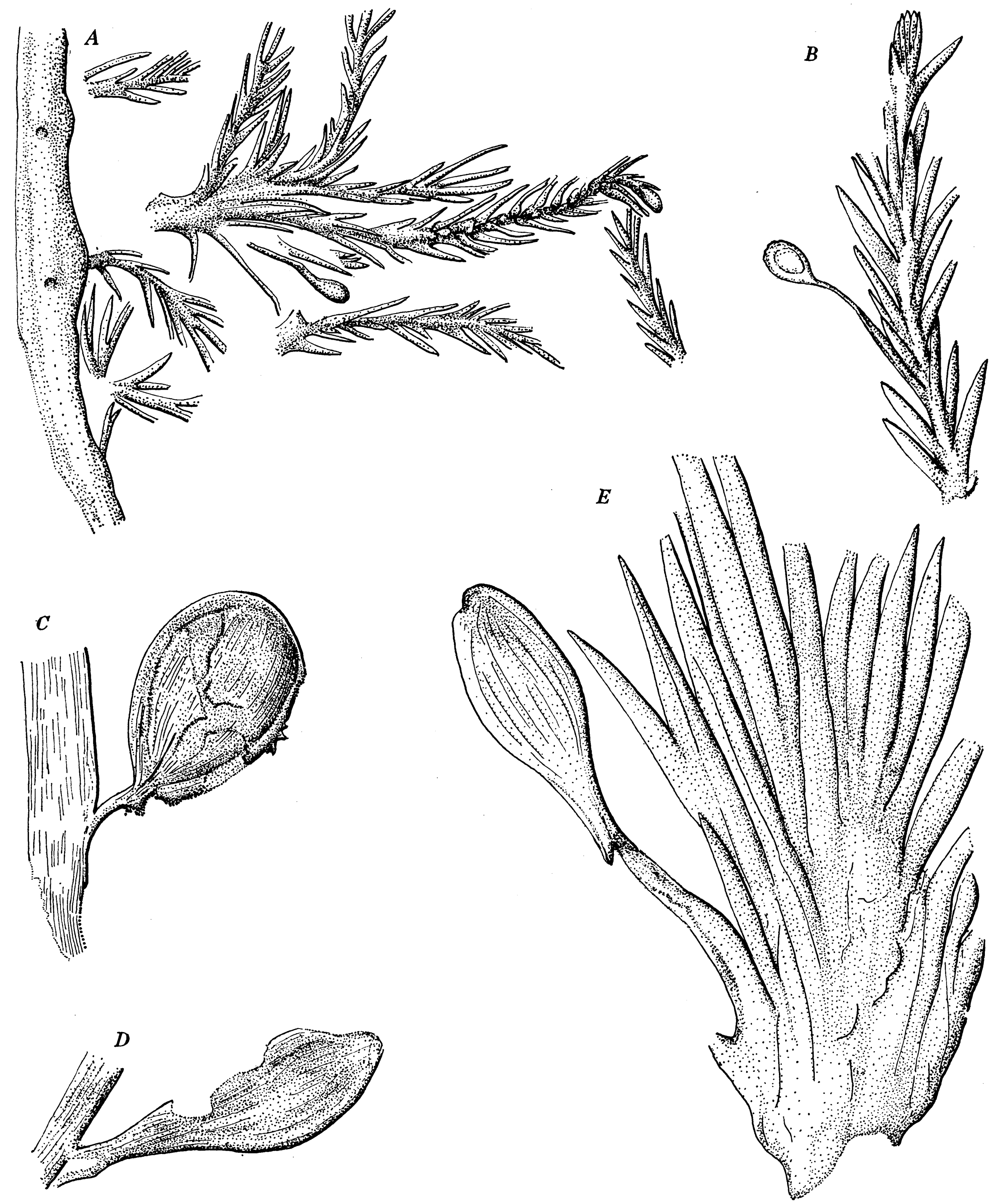



FIGURE 80. Shoots of *Buriadia heterophylla* showing attached seeds. *A*. Irregularly branched shoot whose parent axis shows two branch scars. *B*. Ultimate shoot showing a laterally attached seed and the apical bud (*see* also figures 4, 5, plate 5). *C*. Balsam transfer of an axis bearing a shortly stalked inverted seed (see also figure 6, plate 6). *D*. A portion of an axis bearing a seed (*see* also figure 47, plate 9). *E*. Apical portion of a shoot showing an inverted seed with its a micropylar horn and a slender stalk (*see* also figures 7, 8, plate 6). *A*, specimen 708; *B*, specimen 717; *C*, slide 1215; *D*, specimen 724; *E*, specimen 724. (*A*, *B*, magn. × 1·5; *C*, *D*, × 19; *E*, × 17.)

scarious and hyaline (figure 67, plate 11). They bear small hairs (figures 12, 16, 21, 22, plate 7; figures 79 *E*; 82 *A*, *B*) which are usually more prominent on one of the margins. The surface of the hairs is minutely warty.

All multifid leaves in the type material are situated near the distal end of the leafy lateral branches (figure. 79 *A*). The bilobed leaves are found anywhere with simple ones. One of the bilobed leaves seems to subtend a branch (figure 1 *D*). Multifid leaves may be up to 26 mm long but simple and bifid ones are not more than 15 mm. Smaller forms

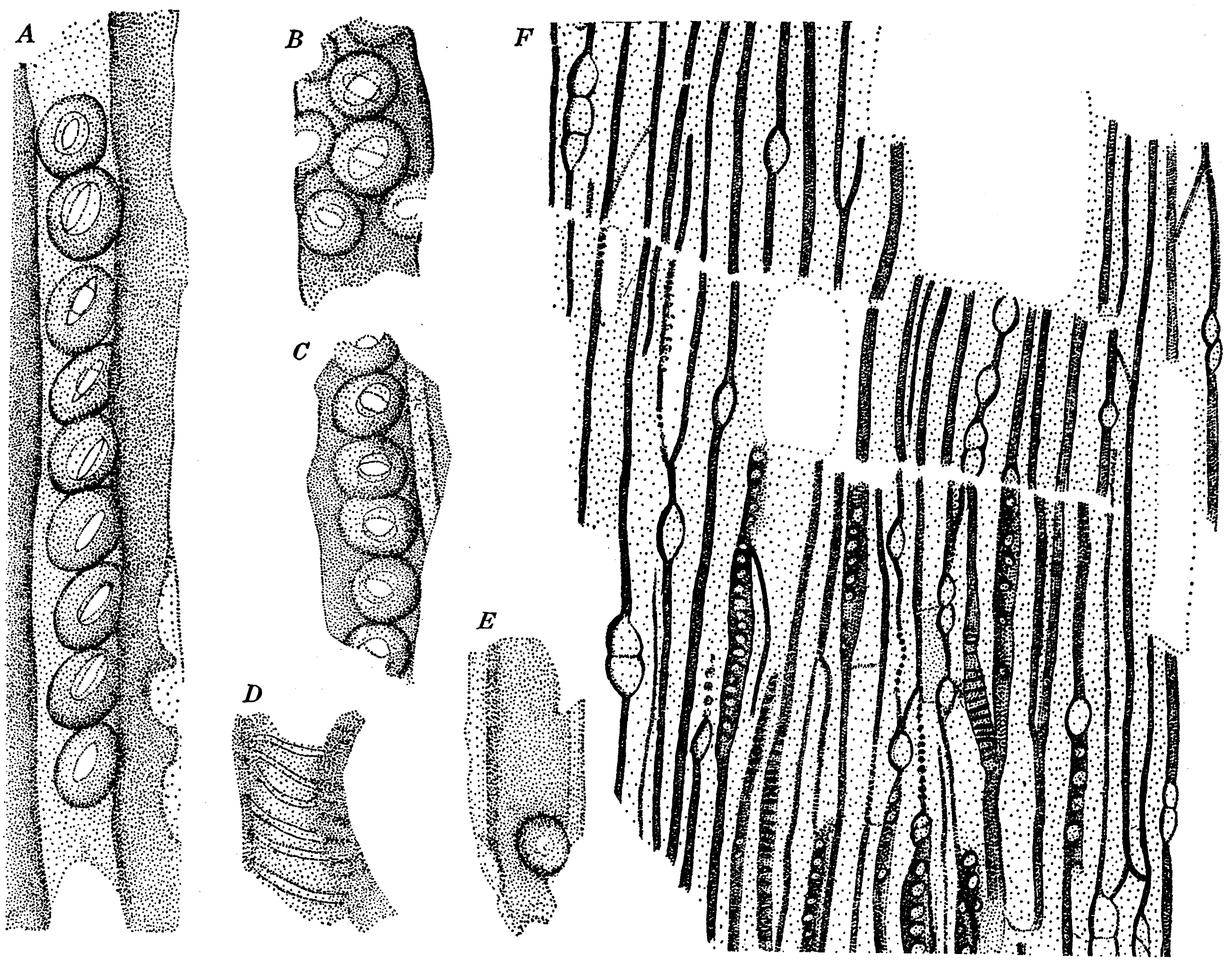



FIGURE 81. *A*. Portion of tracheid showing obliquely placed uniseriate bordered pits. *B*, *C*. Bits of tracheids showing bordered pits with crossed pit pores. *D*. Tracheid showing scalariform thickenings. *E*. A tracheidal fragment showing an isolated bordered pit. *F*. A chip of stem substance showing xylem in tangential section (*see* also figure 34, plate 8). *A* to *E*, slide 830. *F*, specimen 701, slide 701a. (*A* to *E*, magn. × 800; F, × 150.)

of each kind are met and these small leaves may occur on special regions (Feistmantel 1879, pl. 25, figs. 1 to 3). On the analogy of some living lycopods, e.g. *Lycopodium squarrosum* and conifers, e.g. *Araucaria bidwilli* (*see* Dallimore & Jackson 1923), the smaller leaves were probably produced during an unfavourable season of growth. The lamina lacks any superficial marks of veins in bifacial leaves but, the third ridge in trifacial leaves often looks like the midrib. In the distal part of the divided leaves the median ridge also forks into a corresponding number of branches.

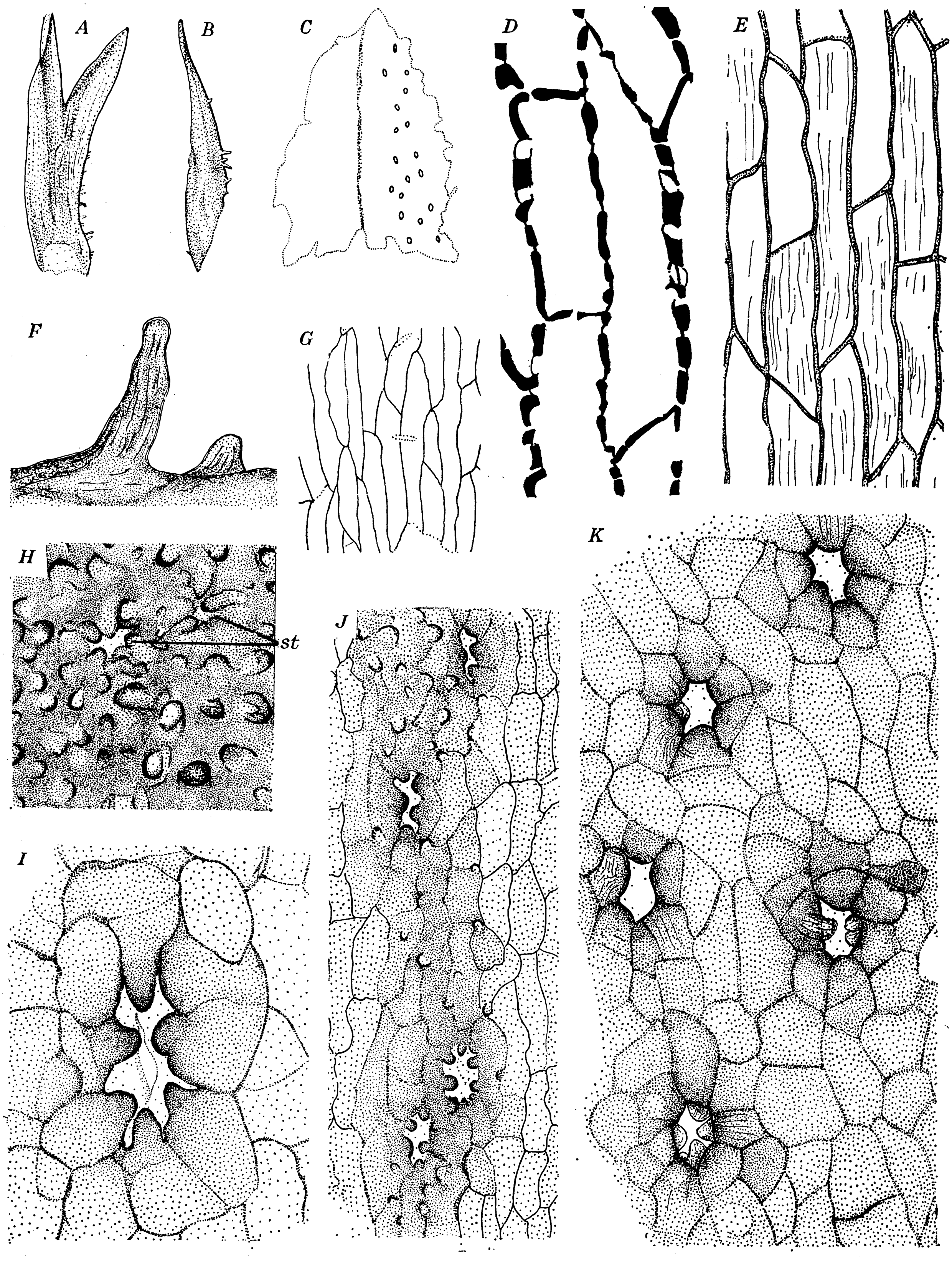



FIGURE 82. *A*, *B*. Bilobed and simple leaves respectively showing marginal hairs (see also figures 12, 22, plate 7). *C*. Cuticle of the apical portion of a bifacial leaf showing the stomatiferous and non-stomatiferous faces (see also figure 38, plate 8). *D*. Cells of the cuticle of non-stomatiferous face showing anticlinal wall pits. *E*. A few cells of non-stomatiferous cuticle of a leaf more magnified to show longitudinal striations (see also figure 35, plate 8). *F*. Cutinized marginal hairs showing longitudinal striations. *G*. Cuticle of non-stomatiferous face in *C*. *H*. Portion of cuticle from the wider stomatiferous band showing rounded papillae partly or completely covering the stomata (*st*) (see also figure 39, plate 8). *I*. Magnified view of stoma to show details. *J*. Portion of the narrower stomatiferous face of leaf showing stomata (see also figure 39, plate 8). *K*. Part of cuticle in *C* showing stomata with clearly differentiated subsidiary cells some of them with elongated papillae (see also figure 48, plate 9). *A*, slide 794; *B*, slide 1225; *C*, slide 750; *D*, slide 741; *E*, slide 761; *F*, slide 1323; *G*, *H*, slide 751; *I*, slide 751; *J*, slide 751 (*A*, *B*, magn. ×10; *C*, ×30; *D*, *E*, ×600; *F*, ×50; *G*, *H*, *J*, *K*, ×300; *I*, ×750).

*Seeds*

A number of otherwise typical shoots in our collection bear solitary ovules on slender stalks of variable length (figure 5, plate 5; figures 6 to 9, plate 6; figures 72 to 74, 78 plate 12; figures 79 *D*, 80 *A* to *E*). Some of these are inserted in the region of an apical bud (figures 7, 8, plate 6; figure 71, plate 11; figure 80 *A*, *E*), but others are borne laterally among the leaves (figure 5, plate 5; figure 80 *A*, *B*) or even on the thicker axes, whose leaves have mostly fallen off (figures 6, 9, plate 5; figure 47, plate 9; figure 72, plate 12; figures 79 *D*, 80 *C*, *D*). They occupy the same position as a leaf and we believe that they are not axillary but replace a leaf in the phyllotactic spiral. The seed is flattened and almond-shaped with a tapering narrow micropylar end and a broadly oval base. The body of the seed is inverted (anatropous), its micropyle pointing towards the parent axis. The two margins form keels (carineae) and one carina (raphe) continues the stalk while the other forms a little horn. The micropyle lies between the stalk and the horn. Detached seeds appear to show two horns but one is the broken stalk (figures 50, 53, 54, 59, 60, plate 10). Some seeds, particularly attached ones, may be flattened in such a manner that the seed stalk and the opposite micropylar horn overlap each other and in these the micropylar horn is not seen (figures 79 *D*, 80 *B*).

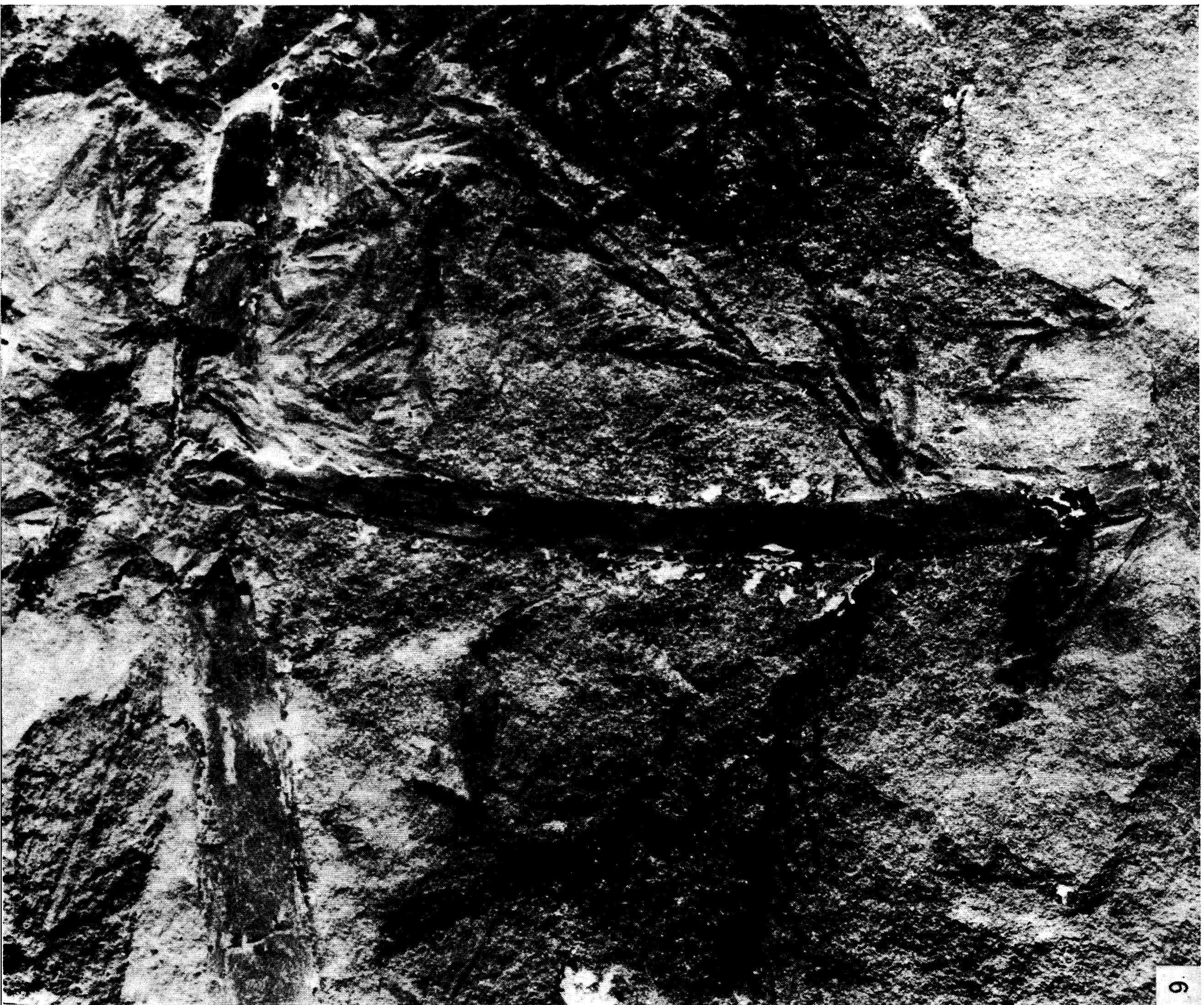
The size of the seeds ranges between 3 to 6 mm in length and 2 to 5 mm in width. About half the specimens of seeds are broadly oval, the rest narrowly oval. These narrower specimens often show prominent longitudinal ridges or carineae in the middle. The broader specimens show narrow marginal borders with hairs and often a shallow longitudinal ridge in the middle. On the basis of Walton's theory of compression (Walton 1936) we conclude that the seeds are platyspermic. When they are compressed along the principal plane they appear wider than when they are compressed along the secondary plane. They have two prominent carineae in the principal plane, which appear like marginal borders when the seeds are compressed along the principal plane, and two low ridges in the secondary plane. The distal end of the seed is rounded or often narrowed out into a short neck like portion (figure 8, plate 6; figure 47, plate 9; figures 51, 55, plate 10). In many seeds the distal end is broken (possibly because of the absence of the tough nucellar cuticle inside) and these show the chalazal hole (figure 52, plate 10; figures 74, 78, plate 12). The surface of the seed shows marginal hairs and longitudinal files of rectangular cells like those seen in other parts of the plant.

## *Internal morphology*

*Stem*

Maceration of the substance of the stem yields a tough surface cuticle and shreds of wood and fibres. The cuticle shows outlines of longitudinally elongated, straight-walled rectangular cells like those seen on the stem surface. Stomata were never observed in the stem cuticle and we presume that the 'indications of several' noticed by Sahni (1928) were not due to stomata if his cuticle was from a stem.

Chips of stem substance failed to show primary wood but the secondary wood is pycnoxylic, the secondary rays being uniseriate (figure 34, plate 8; figure 81 *F*). Tangential views of the wood mostly show one cell high rays, but others are two or three cells in height. Tangential sections of the wood show tracheids with tapering ends and occasional relatively



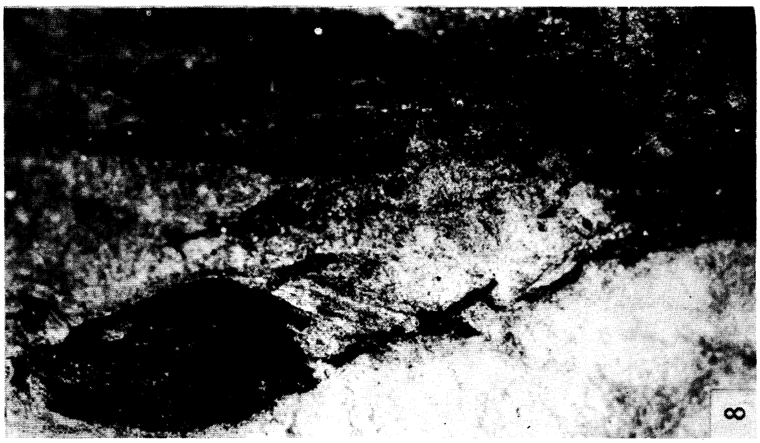


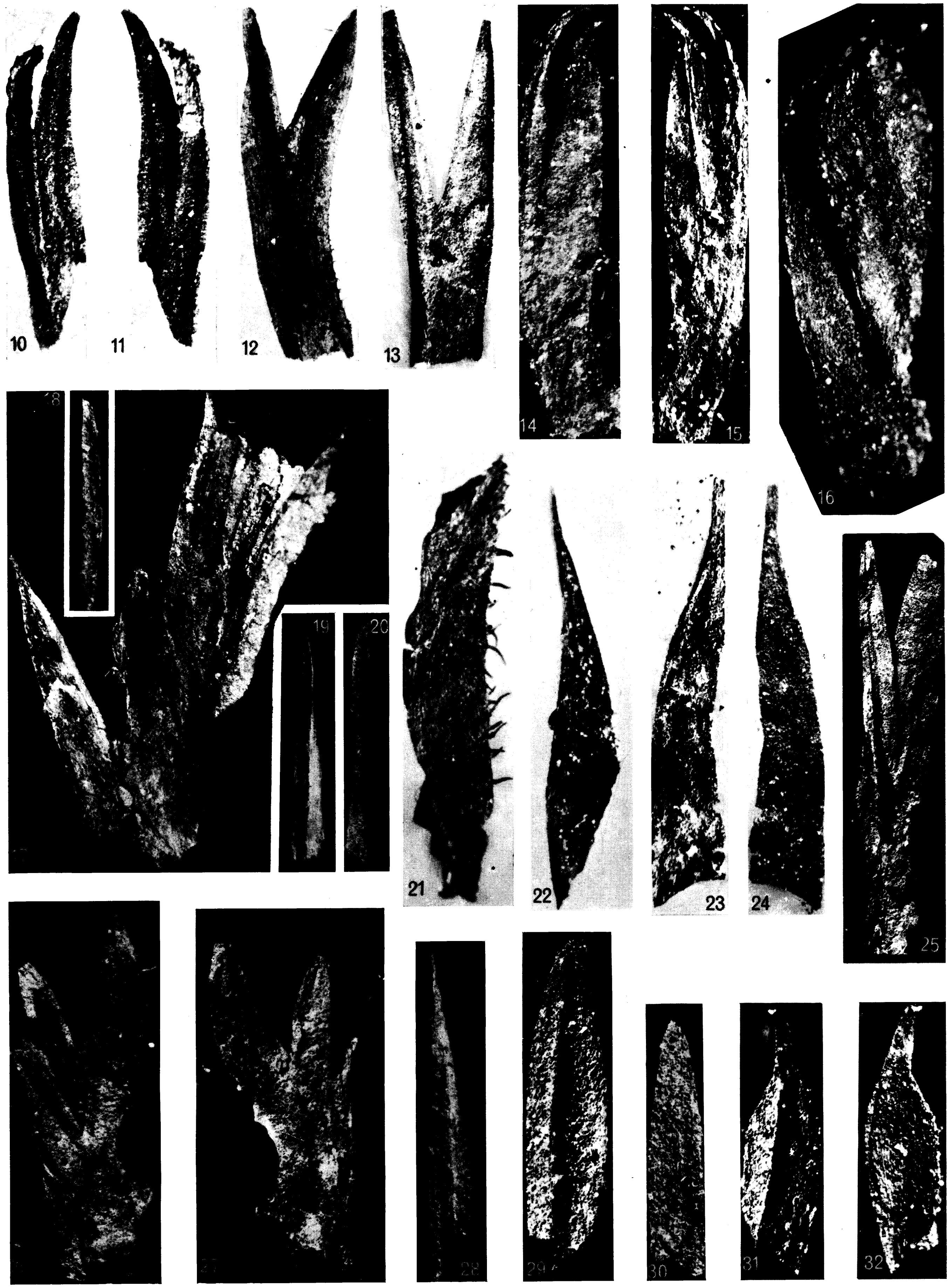
FIGURE 6. Balsam transfer of an axis bearing a shortly stalked inverted seed. Slide 1215. (Magn. × 9)

FIGURE 7. Portion of a shoot showing a recurved seed inserted near an apical cluster of leaves. One of its leaves is distinctly bifid. (Photographed in oil.) Specimen 724. (Magn. × 2.)

FIGURE 8. Apical portion of the shoot in figure 7 more magnified to show the inverted seed with a micropylar horn and the seed stalk. (Magn. × 10.)

FIGURE 9. A shoot with two opposite branches. The central thicker axis shows an attached seed. The surface of the thicker axis is marked with longitudinal lines, some of which enter a side branch (on the left). Specimen 701. (Magn. × 3.)

(*Facing p.* 34)


10
11
12
13
14
15
16
19
20
21
22
23
24
25
28
29
30
31
32

shorter elements of xylem parenchyma having oblique or transverse end walls (figure 34, plate 8; figure 81 *F*). It has not been possible to ascertain the length of the tracheids in the small chips of wood which we studied but the shorter rectangular cells are about 83 μm long and 26 μm wide. The width of the tracheids varies between 16 and 50 μm. The tangential walls of the tracheids are without any pits although the longitudinally cut radial walls (in a tangential section) present sectional views of bordered pits (figure 81 *F*). The same pits when seen in a surface view of the radial wall present a typical rounded or oval outline with a clear border and a central pit pore. The various forms of pits seen on the tracheids are illustrated in figure 81 *A* to *C*, *E*. Only two ray fields were seen and each showed a single widely oval pit pore. With overmaceration the pits are obliquely enlarged and where the pits are crowded the damaged wall appears scalariform, an effect familiar in both rotten wood and in modern wood subjected to severe maceration.

*Leaves*

The cuticle of one (abaxial) face in all leaves of the plant is non-stomatiferous and as a rule tougher than that of the other faces. The non-stomatiferous cuticle shows outlines of longitudinally elongated cells arranged in longitudinal series. Size of the cells ranges between 65 and 179 μm in length and 16 to 39 μm in width. Their anticlinal walls are straight and cross-walls between successive cells of a row may be transverse or oblique. Simple pits are sometimes seen on the anticlinal walls (figure 82 *D*). The cell surface shows fine striations (cutin ridges) running lengthwise (figure 35, plate 8; figure 82 *E*) but no papillae. Near the margins of this face the cells become abruptly narrow. The surface cuticle of many a narrow marginal cell is bulged out to form a short or long cutinized hair (68 to 248 μm long, average 166 μm). There are many more marginal hairs near the leaf base than near the apex.

Various forms of hair are seen in figure 79 *E*. Their surface shows parallel cutin ridges (figure 49, plate 9; figure 82 *F*) which radiate over the cell surface at the base.

One of the two remaining faces in trifacial leaves or the upper face of bifacial leaves

---

Description of plate 7

Figures 10 to 16, 25. Variously flattened bilobed leaves. Figures 10 and 14 are obverse views of two leaves whose reverse views are seen in figure 11 and 15 respectively. The leaves in figures 12 and 16 show a few marginal hairs. Each lobe of leaf in figure 25 shows a ridge. Figures 10, slide 1219; 12, slide 794; 13, slide 1219; 14, slide 1219; 16, slide 728; 25, slide 1221 (10 to 15, magn. ×18; 16, magn. ×40; 25, magn. ×12).

Figure 17. Fragment of a shoot with apical bud (extracted from rock matrix). Slide 1216. (Magn. ×12.)

Figures 18 to 24, 28 to 32. Simple leaves of various shapes and sizes (extracted from the rock matrix). Figures 23 and 31 show obverse faces of leaves whose reverse sides are seen in figures 24 and 32. The leaf in figure 23 is bifacial. The leaf in 31 shows a prominent ridge. Leaves in 21, 22, 31 and 32 show marginal hairs. Figures 18, 19, 20, 28, 30, slide 1219; 21, slide 757; 22, slide 1225; 23, slide 1220; 29, slide 1226; 31, slide 1227; (18 to 20, 28, 30, magn. ×13; 21, magn. ×30; 22, magn. ×18; 23, 24, 29, 31, 32, magn. ×24).

Figures 26, 27. Obverse and reverse views of a shoot (extracted from the rock matrix). 26, slide 1217. (Magn. ×12.)

shows a wide stomatiferous band with narrow non-stomatiferous strips of non-papillate rectangular cells near its two margins. Other ordinary epidermal cells on this face are irregularly arranged. They are short, straight-walled and polygonal. Almost every cell shows a rounded hollow papilla about 10 to 26 $\mu$m $\times$ 10 to 18 $\mu$m in diameter. The papilla may be situated anywhere on the cell surface. The number of papillae decreases considerably near the apex but even here many cells have rounded papillate ends with a thickened cuticle. Elsewhere in the leaf the papillae are so crowded that they often overlap the anticlinal walls of epidermal cells obscuring their outlines from view. Cutin ridges run over these shorter papillae as they do in the longer marginal hairs but as the papillae are rounded structures the ridges over them seem to radiate from their central points (figure 45, plate 9). Numerous irregularly orientated stomata occur scattered between these cells. The cuticle of the third face in trifacial leaves is also delicate and stomatiferous. Its margins are again marked by bands of rectangular cells like those of the second face and in the middle of it runs a narrower, often uniseriate band of stomata which are obliquely or longitudinally orientated. Ordinary epidermal cells of the narrow stomatiferous band are similar to those of the wider band in being polygonal and in having similar rounded papillae although papillate cells are usually less frequent in the narrower bands. According to available details of trifacial leaves it is almost certain that their cross-sections would appear asymmetrical with two unequal stomatiferous faces and a third non-stomatiferous face which was almost as wide as the broader stomatiferous face.

The stomata are haplocheilic, monocyclic or incompletely amphicyclic. They usually show a regular ring of 5 to 7 subsidiary cells and sometimes 2 to 3 encircling cells. The subsidiary cells and also the encircling cells are clearly differentiated from the epidermal cells in being shorter, their size ranges between 18 to 47 $\mu$m tangentially and 18 to 27 $\mu$m

---

Description of plate 8

Figure 33. A portion of a shoot bearing simple as well as bilobed leaves. Specimen 707. (Magn. $\times$ 2·5.)

Figure 34. A chip of stem substance showing tangential view of wood. Specimen 701, slide 701a. (Magn. $\times$ 135.)

Figure 35. Cells of the cuticle of non-stomatiferous face more magnified to show longitudinal striations. Slide 761. (Magn. $\times$ 645.)

Figure 36. Wider papillate face of a leaf as seen under unilateral incident light. Slide 1218. (Magn. $\times$ 135).

Figure 37. Non-stomatiferous face of the leaf in figure 36 showing outlines of cells in unilateral incident light. (Magn. $\times$ 135.)

Figure 38. Cuticle of the apical portion of a bifacial leaf showing the non-stomatiferous and stomatiferous faces. Slide 750. (Magn. $\times$ 46.)

Figure 39. Cuticle of a trifacial leaf. The lower end of the photograph shows the entire covering of the three faces. On the extreme left side is a portion of the cuticle of the non-stomatiferous face partially overlapping the profusely papillate cuticle of the wider stomatiferous face, next to which is seen the cuticle of the narrower stomatiferous face, followed by the remaining part of the cuticle of the non-stomatiferous face, on the extreme right. Slide 751. (Magn. $\times$ 50.)

Figure 40. Part of cuticle of another trifacial leaf. Slide 799. (Magn. $\times$ 35).

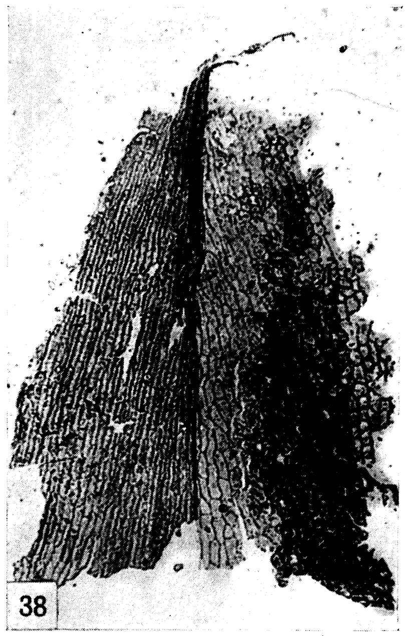

33


34


35

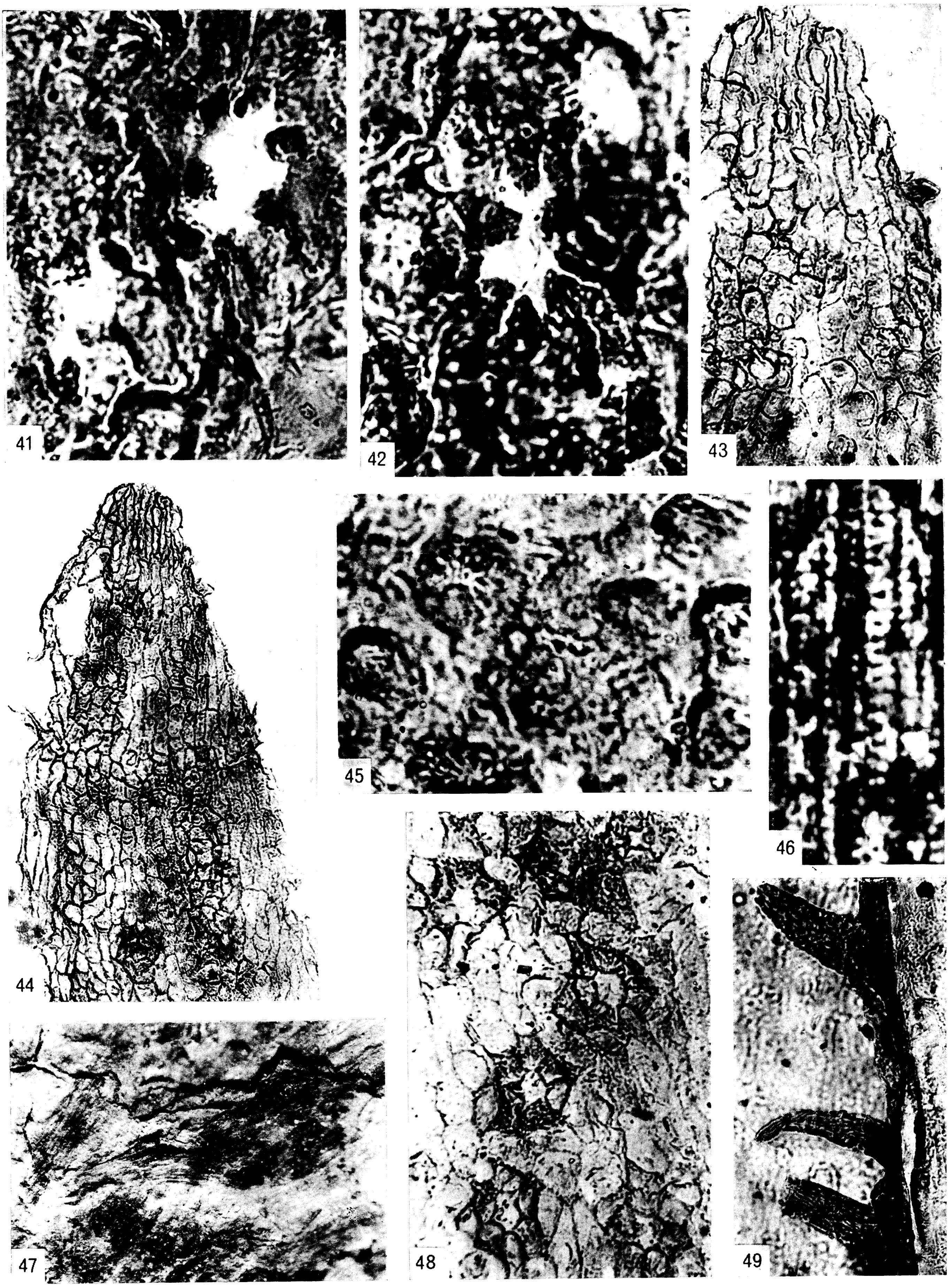

36


37


38


39


40


41
42
43
44
45
46
47
48
49

in width. As a rule, the subsidiary cells are not distinguishable into polars and occasionally a subsidiary cell opposing a pole may be radially elongated (figure 82 *K*). The stomata are sparsely arranged, the closest of them showing at least one intervening cell between their nearest subsidiary cells. The walls of the subsidiary cells are produced into conspicuous hollow papillae which converge over the guard cells to form a more or less crowded canopy (figures 41, 42, plate 9; figure 82 *H* to *K*). The overarching papillae in many stomata, particularly in the wider stomatiferous bands, are so densely crowded that they completely hide the pore and its guard cells (figures 39, 40, plate 8; figure 82 *H*). The surface of the subsidiary cells shows a thicker cuticle which is again marked by cutin ridges radiating round the stomatal pore (figure 82 *K*). The guard cells are sunken in a shallow pit lined by the overarching subsidiaries. In the less well protected stomata part of the guard cell surface may ocasionally be seen but not the outline of the guard cells. The orientation of stomatal pores is more often longitudinal than oblique.

A few leaves seem to have undergone a slow natural maceration before or during fossilization. Their substance is brown and translucent in Canada balsam mounts. The anticlinal walls of their epidermal cells are thicker than those of cell outlines in the cuticle. Through their epidermal coats, a few of them show a single median vascular strand and remnants of the intervening mesophyll tissue. The xylem of the bundle shows narrow scalariform tracheids about 13 $\mu$m wide (figure 46, plate 9). The mesophyll cells are arranged in transverse lamellae (figures 66, 67, plate 11) in the manner of the mesophyll in the leaves of *Pinus*.

*Seeds*

The surface of the seed shows longitudinal rows of rectangular cells all over its surface. The structure of the seed has been studied by maceration of attached specimens and also from detached seeds. In all 22 complete seeds and 20 seed fragments were investigated. Intact micropylar ends were seen in 10 fragments and 2 fragments show chalazal ends.

---

DESCRIPTION OF PLATE 9

FIGURES 41, 42. Stomata from the narrower stomatiferous face in figure 39 showing subsidiary cell papillae overarching the guard cells. (41, 42, magn. × 875.)

FIGURE 43. Stomatiferous cuticle of the apical region of a leaf. Slide 741. (Magn. × 124.)

FIGURE 44. Portion of cuticle in figure 43 more magnified to show details of papillae and stomata. (Magn. × 233.)

FIGURE 45. Portion of cuticle from the wider stomatiferous band in figure 39 showing rounded papillae with radiating striations. (Magn. × 500.)

FIGURE 46. Scalariform tracheids from the median vein of a naturally macerated leaf. Slide 793. (Magn. × 332.)

FIGURE 47. A portion of an axis bearing a seed. Specimen 724. (Magn. × 10.)

FIGURE 48. Part of cuticle in figure 38, showing stomata with less prominent subsidiary cell papillae. (Magn. × 215.)

FIGURE 49. Cutinized marginal hairs of a leaf, showing longitudinal striations. Slide 1223. (Magn. × 150.)

As is usual with seeds some of them are compressed and composed entirely of coaly matter but the hollow interior of others is filled with rock matrix.

Maceration of a seed yields fibres and short sclereids which dissolve in ammonia. Three cutinized sacs remain: (i) a tough outer cuticle of integument, (ii) a delicate inner cuticle of integument next to it, and (iii) a tough nucellar cuticle next to the inner cuticle of integument. The texture of the outer cuticle is smooth but, like the cuticle covering other parts of the plant, it shows longitudinal ridges. The cuticle shows longitudinal rows of rectangular cells like those on the seed surface. The cells over the two faces of the seed are elongated but those over the shallow secondary plane ridges and at the chalazal end tend to be shorter and polygonal (figures 52, 62, plate 10; figure 83 *D*). The cells over the carineae in the principal plane of the seed and over the micropylar tip are much narrower. The surface walls of the cells forming the edge of the carineae often bulge out to form hairs like those found in the leaves. Cells over the two faces of the carineae are also papillate but their papillae are relatively shorter. A few stomata occur towards the carineae and also near the seconday plane ridges (figure 68, plate 11). The form and orientation of stomata is essentially like that of the stomata on the leaves of the plant but the subsidiary cells are less regular.

The cuticle of the seed stalk shows longitudinal rows of elongated cells as in the non-stomatiferous surfaces of the plant. The cell rows in the stalk are continued over the seed.

The second cuticle of the seed which represents the inner lining of integument is also smooth but delicate. It is closely appressed to the surface of the nucellar membrane and

---

### Description of plate 10

Figure 50. Micropylar end of a detached seed showing the truncated stalk and the gradually tapering micropylar horn. Slide 1195. (Magn. × 31.)

Figure 51. Portion of a shoot showing an attached anatropous seed. Specimen 724. (Magn. × 10).

Figure 52. Portion of a seed showing the chalazal hole. Slide 1197. (Magn. × 87.)

Figures 53, 54. Obverse and reverse faces of a detached seed. A ridge towards the left in figure 53 shows a few hairs. One of the forks is gradually tapering. Slide 1185. (53, 54, magn. × 18.)

Figure 55. Attached seed in figures 7, 8, plate 6 magnified to show the median ridge. (Magn. × 12.)

Figure 56. Portion of detached seed showing a large number of marginal hairs. Slide 1224. (Magn. × 21.)

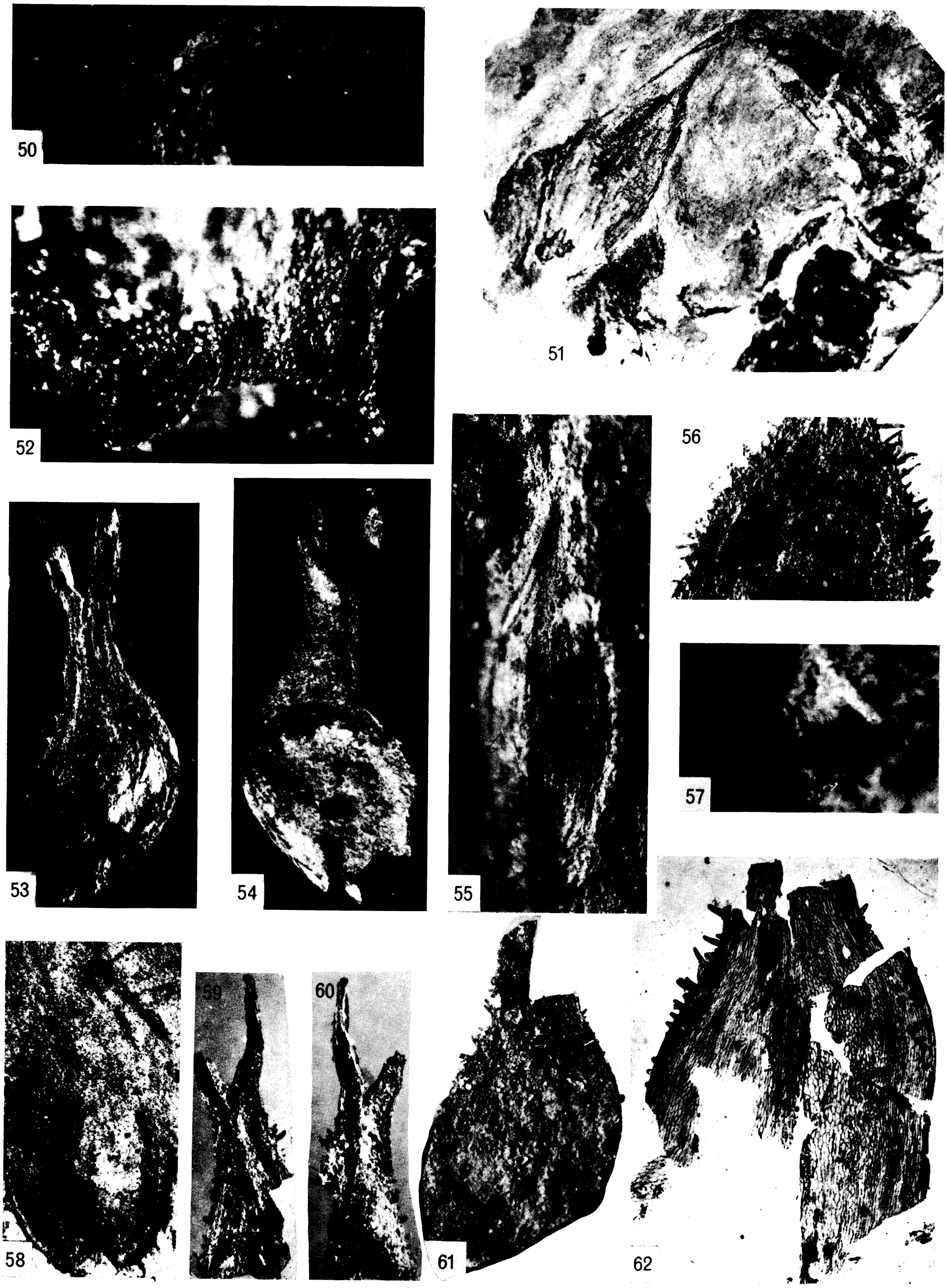
Figure 57. A marginal hair of seed in figure 6, plate 6. (Magn. × 145.)

Figure 58. A detached seed showing a narrow border and hairs along the margins. Its wider end shows a chalazal hole. Specimen 724. (Magn. × 15.)

Figures 59, 60. Obverse and reverse sides of the micropylar end of a detached seed. The margins show a number of hairs and one of its micropylar forks is gradually tapering. Slide 1222. (59, 60, magn. × 20.)

Figure 61. Detached seed with hairy margins. One of its micropylar forks is broken from the very base. Slide 1189. (Magn. × 20.)

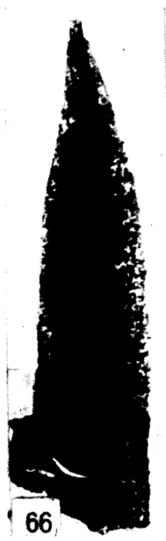
Figure 62. One face of the outer cuticular envelope of integument (obtained by maceration of the seed in figure 61) showing long hairs at the margins and shorter submarginal hairs. (Magn. × 28.)


50
51
52
53
54
55
56
57
58
59
60
61
62


pg
63


pg
64


65


66


68


69


70


71

## Description of plate 11

Figures 63, 64. Fragments of nucellar cuticle with overlapping inner cuticle of integument from micropylar ends of two detached seeds. A few pollen grains (*pg*) are seen inside the tip of the nucellar membrane. Figure 63 shows a portion of the micropylar tube while figure 64 shows fragments of inner cuticle of integument which have partially separated from the nucellar cuticle. 63, slide 1192; 64, slide 1187. (63, 64, magn. × 152.)

Figure 65. Micropylar end of a detached seed, showing marginal hairs. Slide 1222. (Magn. × 17.)

Figure 66. Naturally macerated leaf showing a central dark band (vascular strand) and dark transverse plates of mesophyll tissue through its epidermis. Slide 797. (Magn. × 28.)

Figure 67. Portion of another naturally macerated leaf showing details of mesophyll plates and scarious margin of leaf towards the lower side. Slide 801. (Magn. × 62.)

Figure 68. Outer cuticle of integument of a detached seed showing two stomata. Slide 1187. (Magn. × 250.)

Figure 69. Unwinged, monocolpate pollen grain recovered from the nucellar tip of a detached seed. Slide 1185. (Magn. × 780.)

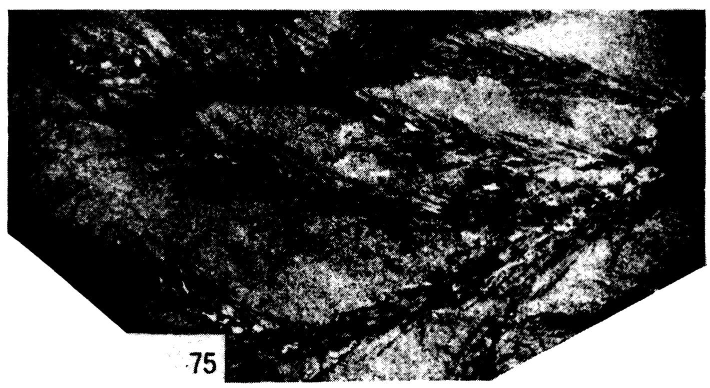
Figure 70. Outer cuticle of integument of a detached seed showing marginal hairs and rows of elongated cells on the surface. Slide 1186. (Magn. × 325.)

Figure 71. Branches of a shoot showing apical clusters of leaves. The bud on the left side shows the end of a seed which is presumably inserted between the leaves. Specimen 1206. (Magn. × 12.)


72


73


74


75


76


77


78

extends all over its surface. Bits of the inner cuticle are sometimes obtained free and in these cell impressions are often obscure, although at some points elongated polygonal outlines may be visible (figure 64, plate 11). The cuticle lining the micropylar canal shows narrower cells. The nucellar cuticle is tough (about 5 μm thick). It extends right up to the chalazal hole and shows clearly marked outlines of longitudinally elongated straight-walled polygonal cells. The size of the nucellar cells ranges between 18 to 48 μm in length and 13 to 23 μm in width (cells in the upper half of the nucellus). The texture of this membrane is coarsely granular and often shows irregular mottlings which appear at places as minute cracks or delicate outlines of unusually small, straight or sinuous-walled cells or as impressions of crystals (figure 83 *K*). The nucellar beak shows converging fimbriate lobes sometimes extending into the base of the micropylar canal (figure 63, plate 11). The tip of the nucellus may have formed an excavated pollen chamber as in many living and fossil gymnosperms.

Pollen grains are usually present inside the cuticle of the nucellar apex. The grains are oval or rounded, monocolpate and smooth walled (figures 63, 64, 69, plate 11; figure 83 *G, H, J, K*). Their size ranges from 55 to 99 μm long to 23 to 83 μm wide. Similar pollen grains have also been found sticking on the surface of the leaf cuticle of the plant. Dispersed pollen grains of this type are called *Ginkgocycadophytus* Samoilowicz. A single seed in figure 54, plate 10, showed a rounded impression in the middle of the seed body. Both its form and location suggested the possibility of its being a megaspore membrane but maceration of the seed did not yield a cutinized megaspore membrane or its remnants.

## Diagnoses

### Genus *Buriadia* Seward & Sahni

*Emended diagnosis*

Shoots woody, irregularly branched, branches bearing leaves in lax or crowded spirals. Wood pycnoxylic. Leaves linear or cuneate, only slightly spreading, simple, forked or multifid, trifacial or bifacial, leaves or leaf segments with a median vein mesophyll in transverse plates. Leaf base decurrent. Stomata haplocheilic, monocyclic or partly amphicyclic. Fertile parts of shoots bearing laterally attached solitary stalked ovules. Ovule anatropous, platyspermic. Body of seed oval with two prominent lateral carineae in

---

### Description of plate 12

Figure 72. Axis with two anatropous seeds. One of them is long stalked and rounded; the other is narrowly oval and shortly stalked, specimen 1225. (Magn. ×4.)

Figure 73. Magnified view of the oval seed in figure 72 to show marginal hairs and the broken micropylar horn. (Magn. ×21.)

Figure 74. Axes with two attached seeds showing chalazal holes at their distal ends. Specimen 1226. (Magn. ×6.)

Figure 75. A penultimate axis with ultimate branches. Specimen 1228 (Magn. ×4.)

Figures 76, 77. Apical portions of two branches showing a few bifid leaves. Specimen 1227 (76, 77, magn. ×4.)

Figure 78. Apical fragment of a shoot showing an inverted seed and its micropylar horn. Specimen 1226. (Magn. ×4.)

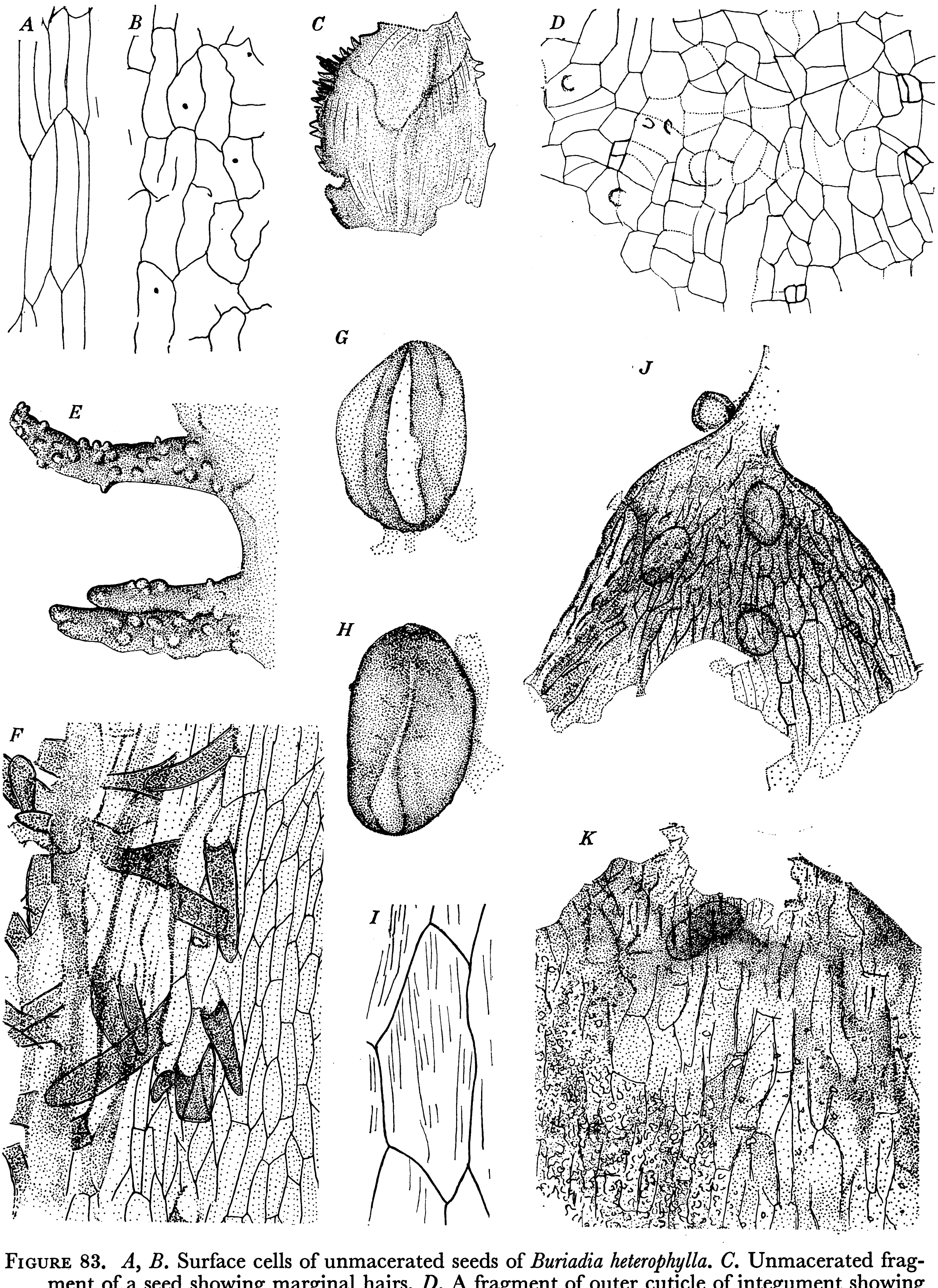



FIGURE 83. *A*, *B*. Surface cells of unmacerated seeds of *Buriadia heterophylla*. *C*. Unmacerated fragment of a seed showing marginal hairs. *D*. A fragment of outer cuticle of integument showing short cells. *E*. Unmacerated hairs of seed showing surface tubercles. *F*. Marginal portion of the outer cuticle of integument showing hairs and rows of narrow elongated cells (see also figure 70, plate 11). *G*, *H*. Unwinged monocolpate pollen grains recovered from the nucellar tips of two seeds. *I*. Magnified view of a cell from outer cuticle of integument showing striations. *J*, *K*. Fragment of nucellar cuticle with overlapping inner cuticle of integument from micropylar ends of two seeds. A few unwinged pollen grains are seen inside the tips of the nucellar membranes. The nucellar cuticle in *J* shows a portion of micropylar tube (see also figure 63, plate 11). *A*, slide 1215; *B*, specimen 724; *C*, specimen 1206; *D*, slide 1185; *E*, slide 1224; *F*, slide 1186; *G*, slide 1192; *H*, slide 1192; *I*, slide 1185; *J*, slide 1192; *K*, slide 1190. (*A*, *B*, *F*, *J*, *K*, magn. × 125; *C*, × 9; *D*, *G*, *H*, *I*, × 500; *E*, × 310.)

principal plane and two low ridges in secondary plane. Chalazal end broadly rounded, micropylar end tapering. Stalk of seed attached in the principal plane, micropyle situated between stalk and opposite horn-like upward prolongation of integument. Integument stony, free from nucellus, internally cutinized. Nucellus with a robust outer cuticle, receiving pollen in its fimbrate apex. Megaspore membrane not cutinized. Pollination typically by *Ginkgocycadophytus* type of pollen grains.

TYPE SPECIES. *Buriadia heterophylla* (Feistmantel) Seward & Sahni.

*Buriadia heterophylla* (Feistmantel) Seward & Sahni
(Plates 4 to 12; figures 79 to 84)

*Voltzia heterophylla* Feistmantel (1879), p. 28, pl. 22, figs. 1–6; p. 23, figs. 1–5; pl. 24, fig. 4; pl. 25, figs. 1–3 (non Brongniart).
*Albertia* sp. Feistmantel (1879,) p. 29, pl. 24, fig. 3; pl. 26, fig. 2.
cf. *Albertia* sp. Feistmantel (1879), p. 29, pl. 24, figs. 1–2.
*Voltzia heterophylla* Arber (1905), p. 216 (pars), fig. 48 (non Brongniart).
*Voltzia*? sp. D. White (1908), p. 569, pl. 8, figs. 11–13*b*.
*Voltzia heterophylla* Lundqvist (1919), p. 21, pl. 2, figs. 14–16 (non Brongniart).
*Buriadia heterophylla* Seward & Sahni (1920), p. 12, pl. 2, figs. 20–25*a*.
*Voltzia* sp. Oliveira (1927), p. 52.
*Buriadia sewardi* Sahni (1928), p. 6, pl. 1, figs. 1–3.
*Buriadia heterophylla* Florin (1940*a*), p. 310, pl. 161–162, figs. 10–23.
*Buriadia heterophylla* Florin (1944*a*), p. 376, text-fig. 11 *a–d*, text-fig. 17 *a–f*, text-fig. 23 *a*, *b*.
*Buriadia heterophylla* Andrews (1955), p. 121.

Similar foliage shoots but with finer details unknown:
*Voltzia heterophylla* Halle (1911), p. 63, pl. 3, figs. 11–15 (non Brongniart).
?*Walchia* sp. Kawasaki & Konno (1932), p. 42, pl. C, figs. 4–5.
?*Walchia* sp. Kawasaki (1934), p. 213, pl. 110, fig. 24.
?*Buriadia* sp. Florin (1940*a*), p. 314.

*Emended diagnosis*

Thicker shoots showing rhomboidal leaf scars and obscure longitudinal ridges. Thinner shoots bearing crowded leaves at a small angle; simple and bifid leaves up to 15 mm long × 0·5 mm broad; multifid leaves up to 26 mm long, their apical lobes spreading to as much as 6·5 mm; simple leaves most frequent, bifid ones less common, multifid ones confined to the apices of a few shoots. Leaf not tapering towards its base, arising from a decurrent cushion. In all leaves one face smooth, other face or faces warty. Margins scarious. Leaves and ovules (occasionally stems also) bearing cutinized hairs at the margins.

Cuticle of stem about 5 $\mu$m thick, non-stomatiferous showing longitudinal rows of rectangular cells, occasionally papillate but usually with longitudinally disposed parallel cutin ridges, anticlinal walls straight, uneven; cuticle of one face of all leaves and interfacial ridges like that of stem. Cuticle of other face or faces stomatiferous, showing irregularly disposed polygonal cells. Outlines of cells often obscured by crowded surface papillae. Stomata longitudinally or obliquely orientated, frequency of stomata 87 mm$^2$ (stomatal index 6·8). Guard cell cuticle thin and hyaline, guard cells usually overarched by subsidiary cells. Stomata often completely hidden by crowded subsidiary cell papillae. Subsidiary cells 5 to 7, usually forming a more or less regular ring, cuticle of subsidiary cells thickened and usually showing radiating cutin ridges; polar subsidiary cells not differentiated, common subsidiary cells between adjacent stomata never seen. Encircling cells like subsidiaries.

Ovules typically 4·5 mm long $\times$ 2·5 mm wide $\times$ 1·5 mm thick. Cuticle of seed stalk and outer cuticle of integument similar to non-stomatiferous cuticles of stems and leaves but showing a few stomata like those of leaves. Inner cuticle of integument thin, sometimes showing obscure polygonal cell outlines; nucellar cuticle showing straight-walled polygonal cells but sides of cells around nucellar break wavy. Pollen grains inside ovule averaging at $74 \times 49$ $\mu$m.

LECTOTYPE Specimen No. 5043 Geological Survey of India, Calcutta (number mentioned by Sahni 5/43).

LOCALITY Buriadih, Giridih coalfield, India.

HORIZON: Lower Gondwana Karharbari beds. (Permo-Carboniferous.)

## DISCUSSION AND COMPARISON

### *General*

Foliage shoots of *Buriadia* were first described by Feistmantel (1879–81) under the names *Voltzia heterophylla* and *Albertia*. A re-examination of Feistmantel's specimens by Seward & Sahni (1920) enabled them to point out several differences between the above shoots and typical northern material of *Voltzia heterophylla* and *Albertia*. In particular, the irregular branching of the shoots and the occurrence of simple and bifid linear leaves as well as some multifid cuneate leaves in the southern shoots prompted them to call the Indian specimens by the name *Buriadia heterophylla*, the type species of their newly founded genus. Later Sahni (1928) figured a small fragment of cuticle which was obtained by macerating a piece of stem from a syntype (specimen 5/38) and changed the name to *B. sewardi*. Subsequently Florin (1940*a*) gave a detailed account of the stomata of some Brazilian shoots referable to the same species which he called *B. heterophylla*. In his detailed account Florin (1940*a*) gave emended diagnoses of the genus and its type species and he also listed under the same species some Korean fossils which had been described earlier by Kawasaki & Konno (1932) and Kawasaki (1934) as possibly belonging to an unnamed species of *Walchia*. At the same time, Florin recognized another doubtful taxon '?*Buriadia* spec.' to which also he referred the above Korean shoots and some fossils described by Halle (1911) from the Falkland Islands.

### *Selection of the lectotype*

As Feistmantel (1879) attributed all material of *Buriadia heterophylla* to *Voltzia heterophylla* he did not mention any type specimen nor did Seward & Sahni (1920) when they referred Feistmantel's Indian material to a new genus, *Buriadia*. In his revision of Indian fossil conifers Sahni (1928) mentions a 'critical specimen' from the type material (pl. I, fig. 1), but he too failed to designate any lectotype. Subsequently, without examining the type material, Florin (1940*a*) mentions a type no. G 289 (pl. II, fig. 20) but as this specimen too has not been categorized as the lectotype and as it does not show diagnostic characters of the genus like cuneate leaves, branching, etc., whereas the specimen termed 'critical' by Sahni does show them rather clearly we have no hesitation in designating specimen no. 5043 from Buriadi, Karharbari (Feistmantel 1879, pl. 23, fig. 2; Sahni 1928, pl. I, fig. 1) as the lectotype. In fact we now find that the specimen even shows two attached seeds. A drawing of the specimen showing all its details accurately is given in figure 79 *A*. Its cuticle agrees in all details with the description and figures of other investigated material referred here to *B. heterophylla*.

*Reasons for referring the new material to* Buriadia heterophylla

The present material is from the same locality as that described by Feistmantel (1879) and by Seward & Sahni 1928. The shoots agree with earlier ones in form and in cuticle and their seeds agree also (though the earlier material had few seeds). We happen to have no shoots with multifid leaves but do not regard this difference as important and we identify our specimens as *B. heterophylla* with confidence. The isolated seeds in our collections match the attached ones perfectly in form and in their structure and we feel certain of their identity. Feistmantel (1882) and Zeiller (1902) have also reported similar detached seeds occurring in association with shoots of *Buriadia* and they even attributed them to *Buriadia*. Florin (1940*a*, 1944*a*) described certain shoots from Brazil as *B. heterophylla* and our work on the Indian cuticles supports this identification but we think the Brazilian material needs further study.

*The systematic position of* Buriadia

Notable morphological characters of *B. heterophylla* are:

A. Irregularly branched woody shoots bearing small spirally arranged leaves. Leaves simple, forked once or forked repeatedly; leaf uncontracted below and arises from a decurrent cushion.
B. Leaf with stomata on upper side (facing stem) but none below. Stomata haplocheilic with a ring of prominently papillate subsidiary cells. Leaf (or leaf lobe) with a single vascular bundle and mesophyll forming transverse plates.
C. Secondary wood pycnoxylic tracheids with uniseriate or multiseriate bordered pits, rays 1 to 3 cells high, ray field with a single pit.
D. Seeds borne singly on stalks among leaves on ordinary shoots. Seeds stalk replacing a leaf in the phyllotactic spiral. Seeds anatropous and platyspermic, margins forming prominent keels, one continuing the stalk, the other extending as a short horn; the micropyle lies between the stalk and horn. Integument cutinized outside and inside; nucellus free to the base, cutinized. Megaspore membrane not cutinized.
E. Pollen occurs in the apex of the nucellus and the grains are monocolpate.

We do not know the main axis of *Buriadia*, but we may imagine it as an upright trunk.

The vegetative characters given above, taken together, point strongly to the conifers. In foliage they agree most closely with the Permian genera *Ernestiodendron* and *Lebachia* (Florin 1938–45) in which most of the leaves are simple but a moderate number of bifid ones occur, at least at certain points, in the branch systems.

There is considerable resemblance between the cuticles (hairs and stomata) of *B. heterophylla* and some of these northern conifers. There are many differences which serve to distinguish them at once. The most obvious is the crowded and regular distichous branches in the lateral shoots of the northern forms; then the distribution of bifid leaves is different (confined to the main axis and certain parts of the female cone in most of the northern ones). There are differences of detail in the cuticles which readily distinguish *Buriadia* at least specifically from each of the numerous northern species. The wood of *Buriadia* is not completely enough known for precise comparison with any particular conifer genus but all its characters are those of conifers (though of course certain other plants like *Ginkgo* have conifer-like wood). We know the structure of the wood even less in the northern forms but some at least (*Walchiopremnon*, see Florin 1940*a*) may be similar. We do not know how *Buriadia* produced its pollen. This is an unfortunate gap in our knowledge. The pollen itself is of the kind most widespread in gymnosperms and does not point to one group rather than another. It occurs in the conifers among several other kinds of pollen. It is noteworthy, however, that a good many of the northern conifers of the Upper Palaeozoic have pollen with some kind of air sac; this is a real difference.

*Buriadia* resembles some southern Lower Gondwana coniferous shoots of *Walkomiella australis* and *Paranocladus* in its irregular branching, cuticular structure and hairs. However, neither *Walkomiella* nor *Paranocladus* possess bifid leaves. A fertile shoot of *W. indica* described by Surange & Singh (1953) resembles *Buriadia* even in bearing seeds among the leaves near its apex but this isolated fertile fragment is so small that it could even represent a short shoot of a compound *Lebachia*-like cone. Moreover, there are differences of detail between the cuticles of *W. indica* and *Buriadia*. *W. indica* has 1 to 3 celled hairs, epidermal cells with sinuous and often smooth anticlinal walls and orthotropous seeds.

The most striking difference between *Buriadia* and a typical conifer is the way in which the seeds are borne but the stalked seeds themselves appear closely similar to those of certain northern conifers (with anatropous stalked ovules) though others with erect orthotropous ovules are less similar. However, even the most similar of these, for instance, *Walchiostrobus* sp. (Florin 1940*a*, pl. 153, fig. 4 and text-fig. 34, i) and *Walchia* (*Ernestiodendron germamica* Florin 1939*c*, pl. 149 and text-fig. 35) lack the little horn on the side of the micropyle opposite the stalk. We do not know much about the seed cuticles of the northern conifers, but various recent and fossil conifers have a free nucellus cutinized to the base, as in *Buriadia*. The absence of a megaspore membrane cuticle is an unexpected and unexplained difference between *Buriadia* and most conifers and indeed most gymnosperms; though a few like *Taxus* have virtually none.

Thus no conifer, except perhaps *Walkomiella indica*, bears its ovules in the way they are formed in *Buriadia*, just a simple stalked ovule replaces a leaf here and there on an ordinary leafy shoot. At first sight this seems to separate *Buriadia* with no 'cone' at all from all conifers in which the ovules are borne on lateral organs of fundamentally complex nature—and usually aggregated on special reproductive shoots called cones. Equally, it is separated from the taxads where the ovules are terminal on little shoots, and indeed the separation from the taxads is so fundamental that we will not consider them further. The difference from the conifers too may be fundamental, in which case *Buriadia* would represent yet another group of plants presumed to be unrelated to anything else because of the

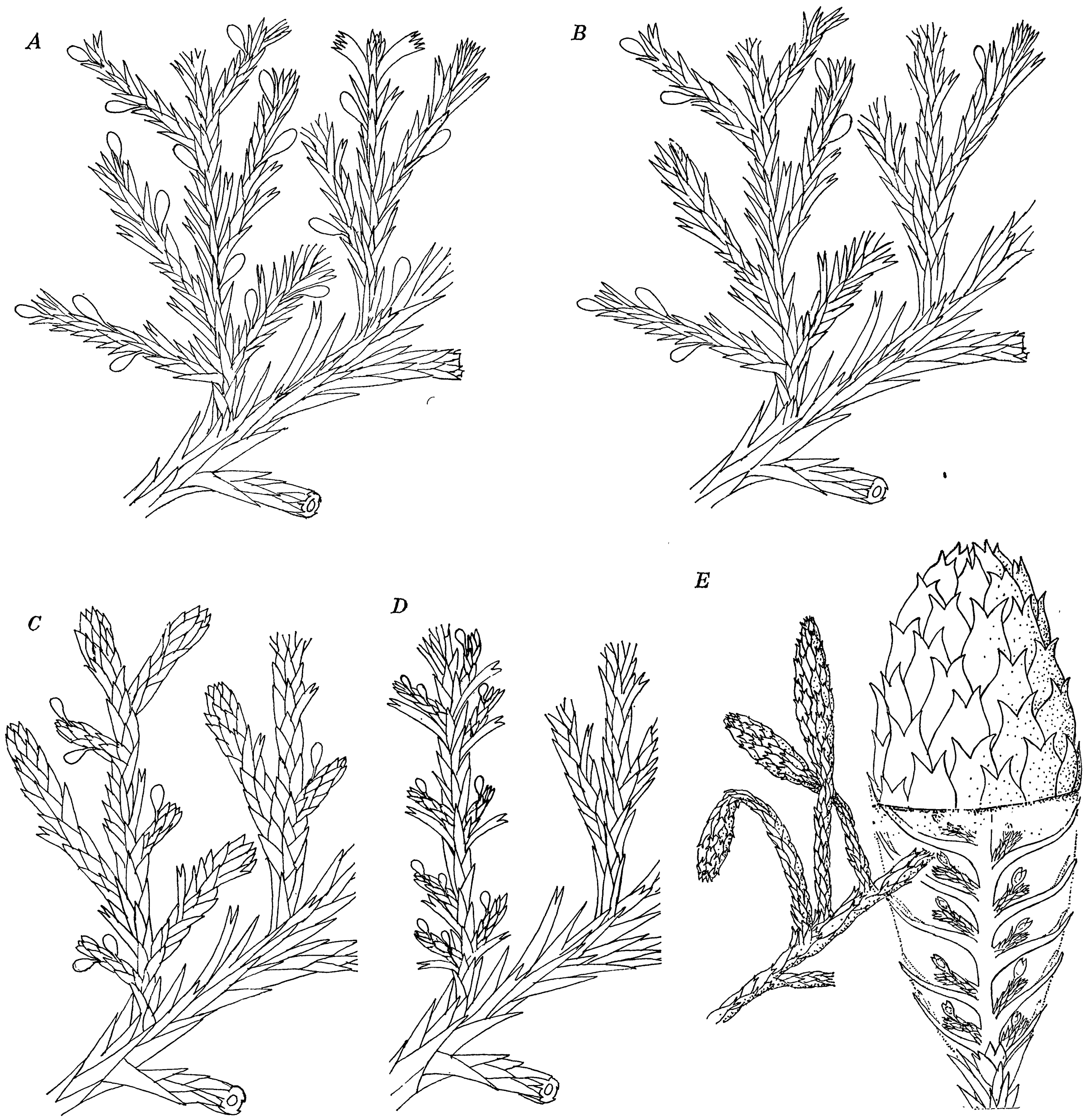



FIGURE 84. Diagrammatic representation of the supposed stages in the evolution of the coniferous cone from a *Buriadia*-like ancestor. *A*. Shoot of *Buriadia heterophylla* with laterally attached isolated seeds on branches of all orders. *B*. Axis of a plant (hypothetical) with seeds attached as in *Buriadia* but borne only on some unreduced lateral branches as in *Buriadia*. *C*. Axis of a plant (hypothetical) with reduced fertile branches. *D*. Hypothetical plant as *C*, but fertile shoots clustered around a specialized lateral branch. *E*. A shoot of *Lebachia piniformis* with terminal cones on lateral branches. The longitudinally split 'cone' on the right side shows a series of fertile short shoots as in *C* but these are further reduced, closely packed and protected by the subtending bracts. (*E*, based on Florin's description and figures.)

morphological difficulty of bridging the gap in one particular organ between it and other forms with which it agrees in other respects. This may indeed be the right conclusion but the resemblances of *Buriadia* to the conifers in general and to contemporary conifers in particular are so close that it is reasonable to follow alternative possibilities vigorously.

It is possible to compare the fertile shoot of *Buriadia* with the fertile dwarf shoot of members of the *Walchia* group. In the *Walchia* group the large cone consists of an axis bearing small, crowded fertile short shoots. Each of these arises in the axil of a leaf (usually bifid) and consists of a short stem of unlimited growth. In the different species it bears various numbers of little pointed leaves and stalked ovules; in some leaves are lacking. The whole dwarf shoot is flattened but seems to be of fundamentally radial construction.

We may imagine the primitive ancestor of *Walchia* as a conifer with simple or forked leaves and unreduced fertile shoots, in fact something looking almost exactly like *Buriadia*. Its fertile shoots would then have been just ordinary shoots, not at all aggregated into clusters or cones. Evolution could have proceeded by the differentiation of sterile and fertile shoots and then by the reduction of the fertile shoots in size (and number of leaves, by failure of their apices to continue growth). Thus a difference could have arisen between vegetative (unlimited) and fertile shoots. Then, or at the same time, the fertile shoots could have aggregated with similar fertile shoots to give a compact cluster and the axis of this compact cluster itself would normally be limited in growth. We would now have something very close to *Lebachia* or *Ernestiodendron* (cones of the *Walchia* group). A further change needed is a little flattening of the fertile dwarf shoot in its crowded position. It is easy to imagine that this crowding would give a conifer advantages of protection over *Buriadia* which has unusually exposed ovules.

Certain other possibilities should be mentioned, even if only to dismiss them. *Buriadia* could be compared with various podocarps which have ovules borne singly on stalks in a scarcely specialized shoot. It would be even possible to compare the horn with the podocarp epimatium. In podocarps, however, the stalk is thick and there is much evidence for regarding it as a reduced form of a complex structure, in fact a conifer fertile dwarf shoot, of which the epimatium represents a leaf. The whole organ is axillary, it does not replace a leaf. We see no reason for considering *Buriadia* as a plant reduced from anything like the modern podocarp; reduced indeed to such an extent that all signs of its complex nature have vanished. Such a view is possible but has nothing to commend it.

*Buriadia* could be compared with the Ginkgoales, in which the leaves are normally forked, and usually forked many times and the ovules are borne on a stalked structure, not in cones. But the seed-bearing stalk of *Ginkgo* is itself axillary and the way it bears its seeds is not similar. Comparison of single parts of *Buriadia* with single parts of other living and fossil plants is easy and some of the resemblances are indeed close, but such comparison is scarcely worth making unless there is at least moderate agreement in other organs. After all plants are related (and classified) as whole plants and not on thoughts about single organs and in total disregard of other facts.

## Summary

Numerous well preserved compressions of shoots referable to *Buriadia heterophylla* (Feistmantel) Seward & Sahni are described from the type locality, Buriadih in the Giridih coalfield. The new hand specimens are remarkable for showing numerous platyspermic seeds some of which are actually attached to the shoots of *Buriadia*. As a result of the investigation of the new duplicates and a re-examination of the type material, several hitherto unknown structural details of the plant are described. The secondary wood of the stems is pycnoxylic having only shallow uniseriate rays. The radial walls of the tracheids show uniseriate or multiseriate bordered pits. The plant shows trimorphic leaves which may be bifacial or trifacial. The abaxial faces of all leaves are non-stomatiferous but the remaining side or sides show numerous stomata and papillate epidermal cells. The stomata are haplocheilic and monocyclic or incompletely amphicyclic. Their subsidiary cells are prominently papillate. The guard cells are sunken and overarched by subsidiary cell papillae. Prominent hair-like papillae are present at the margins of the non-stomatiferous face. Naturally macerated leaves show mesophyll cells arranged in transverse plates and a single median vein with scalariform tracheids.

Seeds are borne on slender stalks whose proximal ends are inserted singly among the leaves. The seeds are anatropous and their micropyles lie between a micropylar horn and seed stalk. Maceration of a seed yields three cuticles (i) an outer cuticle of integument which shows hair-like papillae and stomata of the same type as are found in the leaves, (ii) a thin inner cuticle of integument rarely showing polygonal cells, and (iii) a tough nucellar membrane with elongated polygonal cells. The nucellar tip (pollen chamber) often contains oval monocolpate pollen grains of *Ginkgocycadophytus* type.

The relationships of *Buriadia* are discussed in detail. The occurrence of pitted secondary xylem in its stem, its resistant cuticle and naked seeds with pollen in the nucellar tips make it certain that *Buriadia* was a gymnosperm. Externally, the shoots of *Buriadia* are rather like those of some Permian conifers of the *Walchia* group and they also resemble them in their cuticular structure and hairs. The pycnoxylic wood of *Buriadia* is also comparable with that of the conifers but it forms no female cones of the type met with in the Permian or modern members of the Coniferales. Instead, it bears its seeds singly on ordinary shoots among the leaves. This may either mean that *Buriadia* is an unusual conifer or that it is unclassifiable amongst the presently known groups of the gymnosperms. Pollen producing organs of *Buriadia* are so far unknown.


We owe a deep debt of gratitude to Professor T. M. Harris, F.R.S., for critical suggestions. Our thanks are also due to Professor R. Florin, Professor John Walton and Professor R. Kräusel for their suggestions. We thank Drs G. K. Srivastava and B. K. Verma for help in the collection of material. Dr A. G. Jhingran, Director-General, Geological Survey of India, Calcutta, kindly permitted us to study the type collection located in the Palaeontology Section of the G.S.I. where Messrs M. V. A. Shastri and S. C. Pant provided the necessary facilities—we have great pleasure in acknowledging their help. We must also record our deep appreciation of the ready help given by Messrs V. D. Mamgain, P. R. Chandra, P. P. Satsangi, S. C. Shah and J. N. Dhaundiyal at the G.S.I. laboratories.

We thank the Council of Scientific and Industrial Research, New Delhi, for financing a Research Scheme under the senior author (D. D. P.) and the University Grants Commission for two grants of Rs. 1500 and Rs. 500 in aid of our work.

## References

Andrews, H. N. 1955 Index of generic names of fossil plants, 1820–1950. *Bull. U.S. Geol. Surv.* no. 1013, 1–262.

Arber, E. A. N. 1905 *Catalogue of the fossil plants of the of the Glossopteris flora in the Department of Geology, British Museum (Nat. Hist.).* lxxiv + 255 pp. London.

Dallimore, W. & Jackson, A. B. 1923 *A handbook of Coniferae including Ginkgoaceae.* xi + 570 pp. London.

Feistmantel, O. 1879 The fossil flora of the Gondwana System, **3** (Lower Gondwanas), Pt. 1. The flora of the Talchir–Karharbari beds. *Palaeont. indica* (Ser. 12), pp. 1–64.

Feistmantel, O. 1880–81. The fossil flora of the Gondwana System, **3** (Lower Gondwanas), Pts. 2 and 3. The flora of the Damuda–Panchet Divisions. *Palaeont. indica* (Ser. 12), pp. 1–149.

Feistmantel, O. 1882 The fossil flora of the Gondwana System, **4**, Pt. 1. The fossil flora of the South Rewah Gondwana Basin. *Palaeont. indica* (Ser. 12), pp. 1–52.

Florin, R. 1938–45 Die Koniferen des Oberkarbons und des unteren Perms. Pts. 1–8. *Palaeontographica*, B **85**, 1–730. (1938, Pt. 1: 1–62; 1939*a*, Pt. 2: 63–122; 1939*b*, Pt. 3: 123–174; 1939*c*, Pt. 4: 175–242; 1940*a*, Pt. 5: 243–364; 1944*a*, Pt. 6: 365–456; 1944*b*, Pt. 7: 457–654; 1945, Pt. 8: 655–730.)

Florin, R. 1940*b* On *Walkomiella* n.gen., a genus of Upper Palaeozoic conifers from Gondwanaland. *K. Svenska Vet.-Akad. Handl.* (Ser. 3) **18** (5), 1–23.

Florin, R. 1940*c* The Teriary fossil conifers of South Chile and their phytogeographical significance, with a review of the fossil conifers of southern lands. *K. Svenska Vet.-Akad. Handl.* (Ser. 3), **19** (2), 1–107.

Halle, T. G. 1911 On the geological structure and history of the Falkland Islands. *Bull. Geol. Inst. Univ. Uppsala* **11**, 115–229.

Kawasaki, S. 1934 The flora of the Heian System. Pt. 2. *Bull. Geol. Surv. (Korea) Chosen* **6** (4), 46–311.

Kawasaki, S. & Konno, E. 1932 The flora of the Heian System. Pt. 3. *Bull. Geol. Surv. (Korea) Chosen* **6** (3), 31–44.

Lundqvist, G. 1919 Fossile Pflanzen der Glossopteris Flora aus Brasilien. *K. Svenska Vet.-Akad. Handl.* **63** (3), 1–36.

Oliveira, E. P. de 1927 Geologia e recursos mineraes do estado do Paraná. *Monogr. Serv. Geol. e Mineral do Brasil* no. 6.

Sahni, B. 1928 Revisions of Indian fossil plants. Pt. 1. Coniferales (*a*, Impressions and incrustations). *Palaeont. indica* (N.S.) **11**, 1–49.

Sahni, B. 1931 Revisions of Indian fossil plants. Pt. 2. Coniferales (*b*, Petrifactions). *Palaeont. indica* (N.S.) **11**, 50–124.

Seward, A. C. & Sahni, B. 1920 Indian Gondwana plants: a revision. *Palaeont. indica* (N.S.) **7**(1), 1–41.

Shah, S. C. & Singh, G. 1965 Observations on *Moranocladus oldhami* (Zeiller)—an appraisal of the genus *Moranocladus*. *Curr. Sci.* **34** (7), 215–216.

Surange, K. R. & Singh, P. 1953 The female dwarf shoot of *Walkomiella indica*—a conifer from the Lower Gondwanas of India. *Palaeobotanist* **2**, 5–8.

Walton, J. 1936 On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic equisetalean genus *Annularia* Sternberg. *Phil. Trans.* B **226**, 219–237.

White, D. 1908 Fossil flora of the Coal-Measures of Brazil. In White, I. C., *Comissao Estudos das Minas de Carvao de Pedra do Brazil.* Final report, Pt. 3, pp. 337–617.

Zeiller, R. 1902 Observations sur quelques plantes fossiles des Lower Gondwanas. *Palaeont. indica* (N.S.) **2**, 1–40.

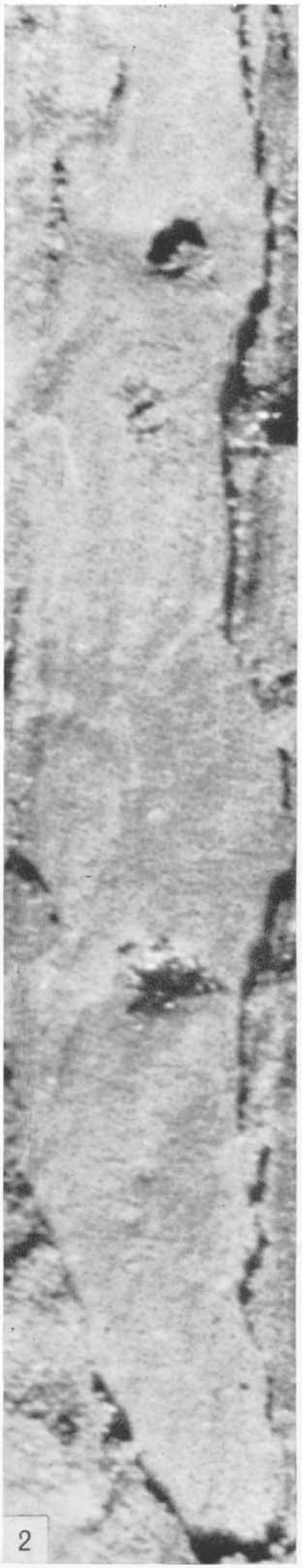


FIGURE 1. Compressions of foliage shoots. Specimen 710. (Magn. × 3.)

FIGURE 2. A thicker axis showing branch scars. Specimen 708. (Magn. × 5.)


FIGURE 3. Twice branched longitudinally ribbed fragment of a shoot. The ovoid scars seen on the leafless shoot of the first order and also on one of its leafy branches are brownish spots on the rock. Specimen 694. (Magn. × 1·5.)

FIGURE 4. Branching foliage shoots, one of them with an attached seed. A thick leafless axis (towards the left) and a detached seed are also seen. Specimen 717. (Magn. × 0·8).

FIGURE 5. Portion of a branched shoot in figure 4, more magnified to show the attached seed (*s*), and the apical bud. A detached seed (*ds*) is also seen. (Magn. × 3.)

FIGURE 6. Balsam transfer of an axis bearing a shortly stalked inverted seed. Slide 1215. (Magn. × 9)

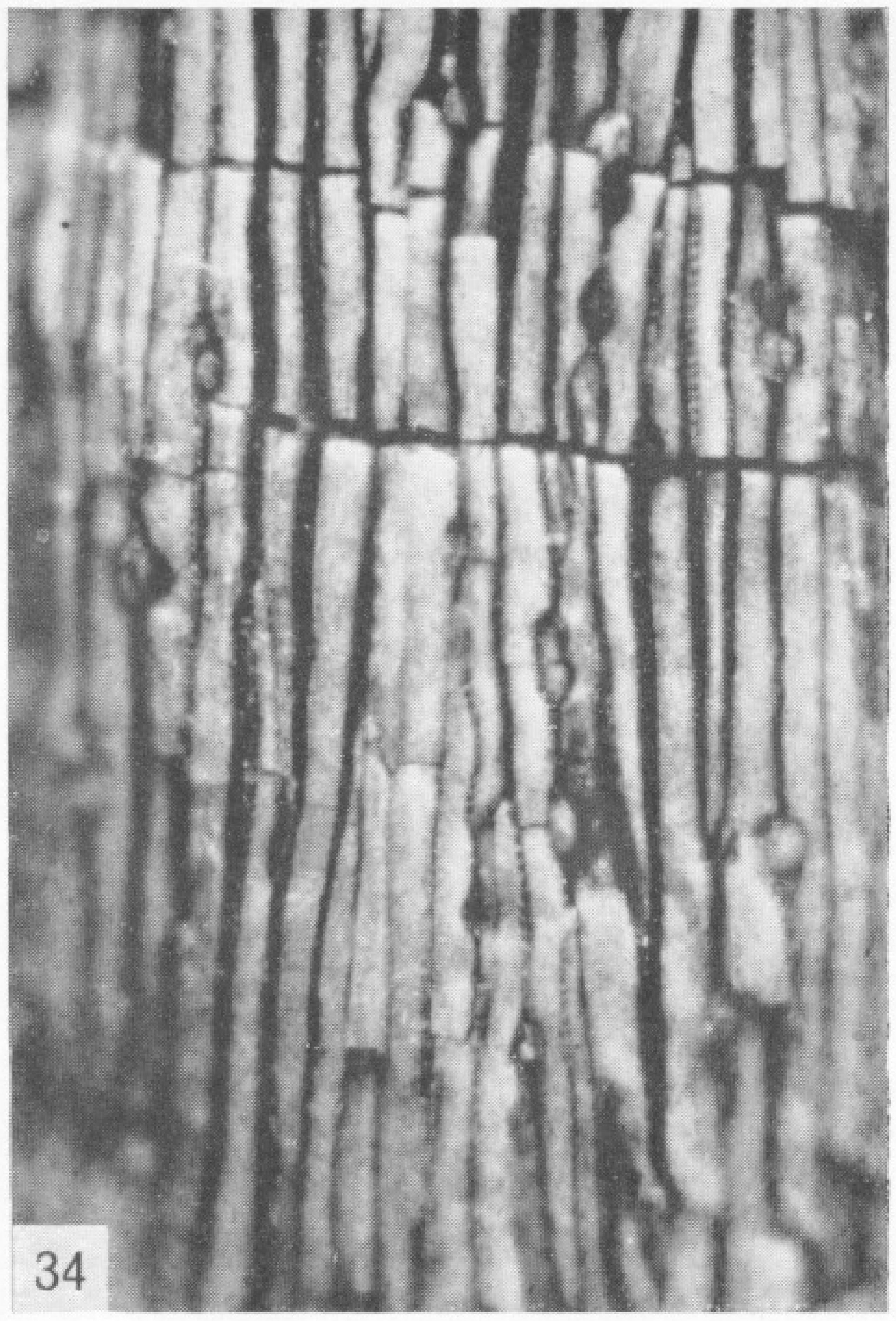
FIGURE 7. Portion of a shoot showing a recurved seed inserted near an apical cluster of leaves. One of its leaves is distinctly bifid. (Photographed in oil.) Specimen 724. (Magn. × 2.)

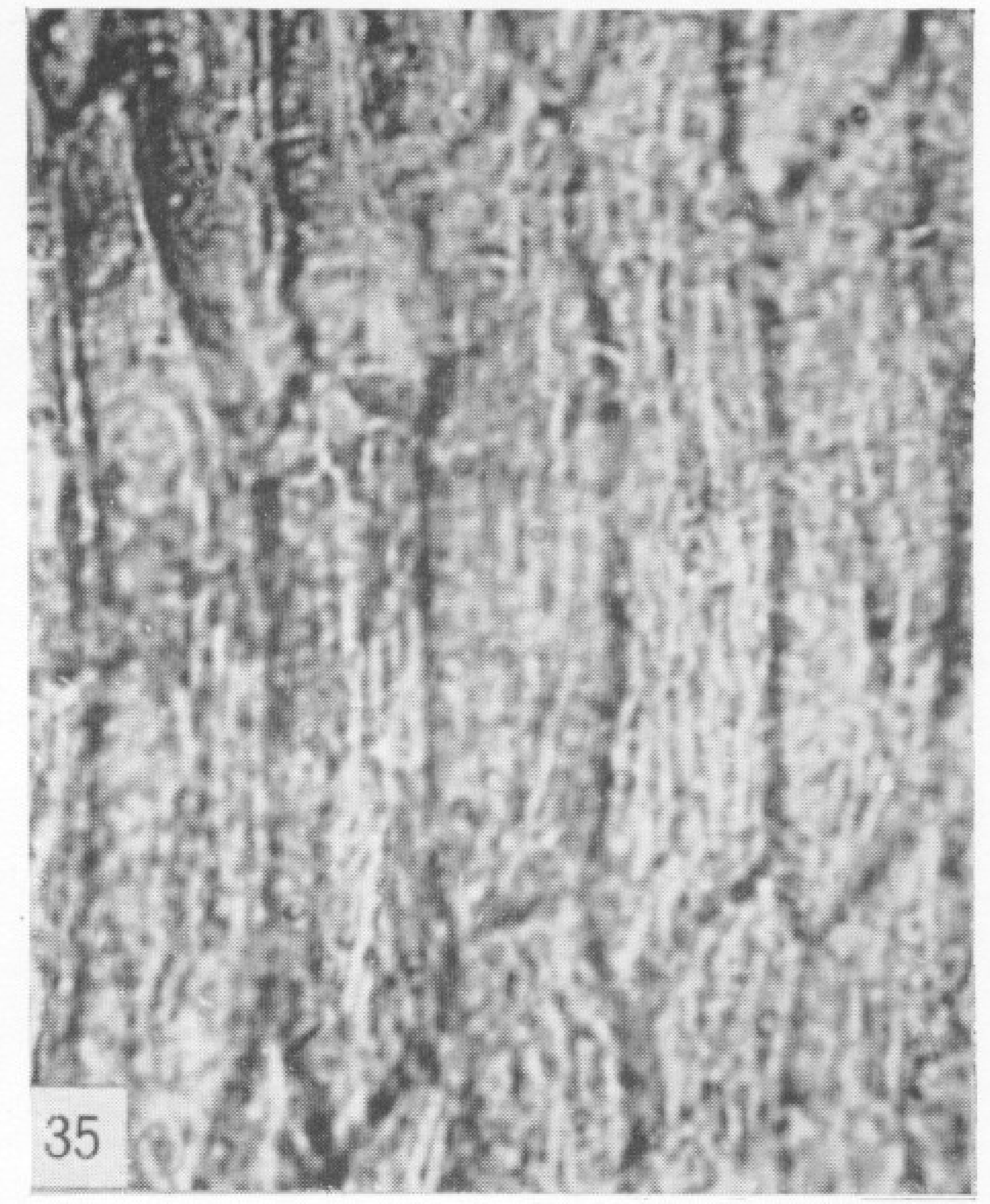
FIGURE 8. Apical portion of the shoot in figure 7 more magnified to show the inverted seed with a micropylar horn and the seed stalk. (Magn. × 10.)

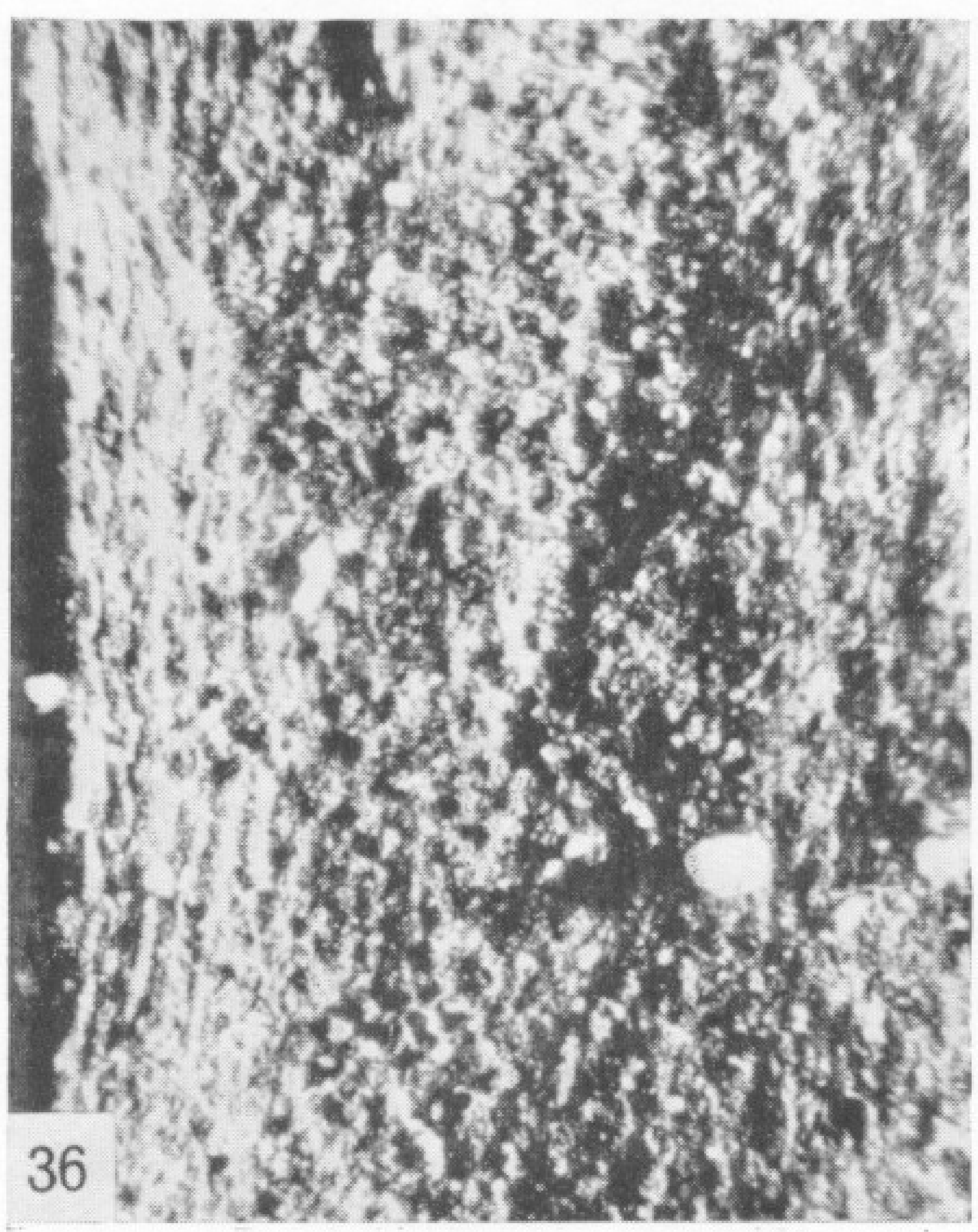
FIGURE 9. A shoot with two opposite branches. The central thicker axis shows an attached seed. The surface of the thicker axis is marked with longitudinal lines, some of which enter a side branch (on the left). Specimen 701. (Magn. × 3.)

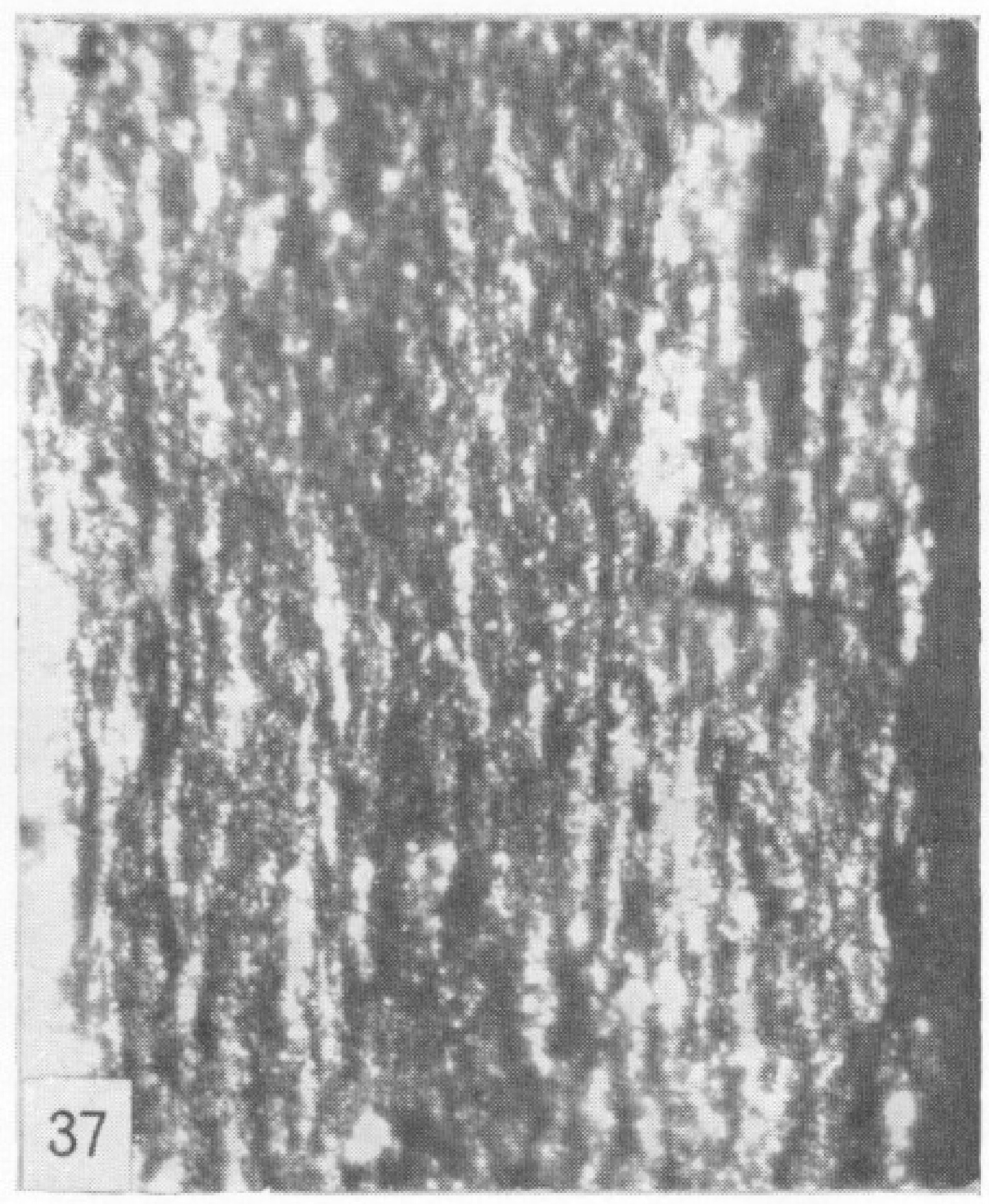

10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32

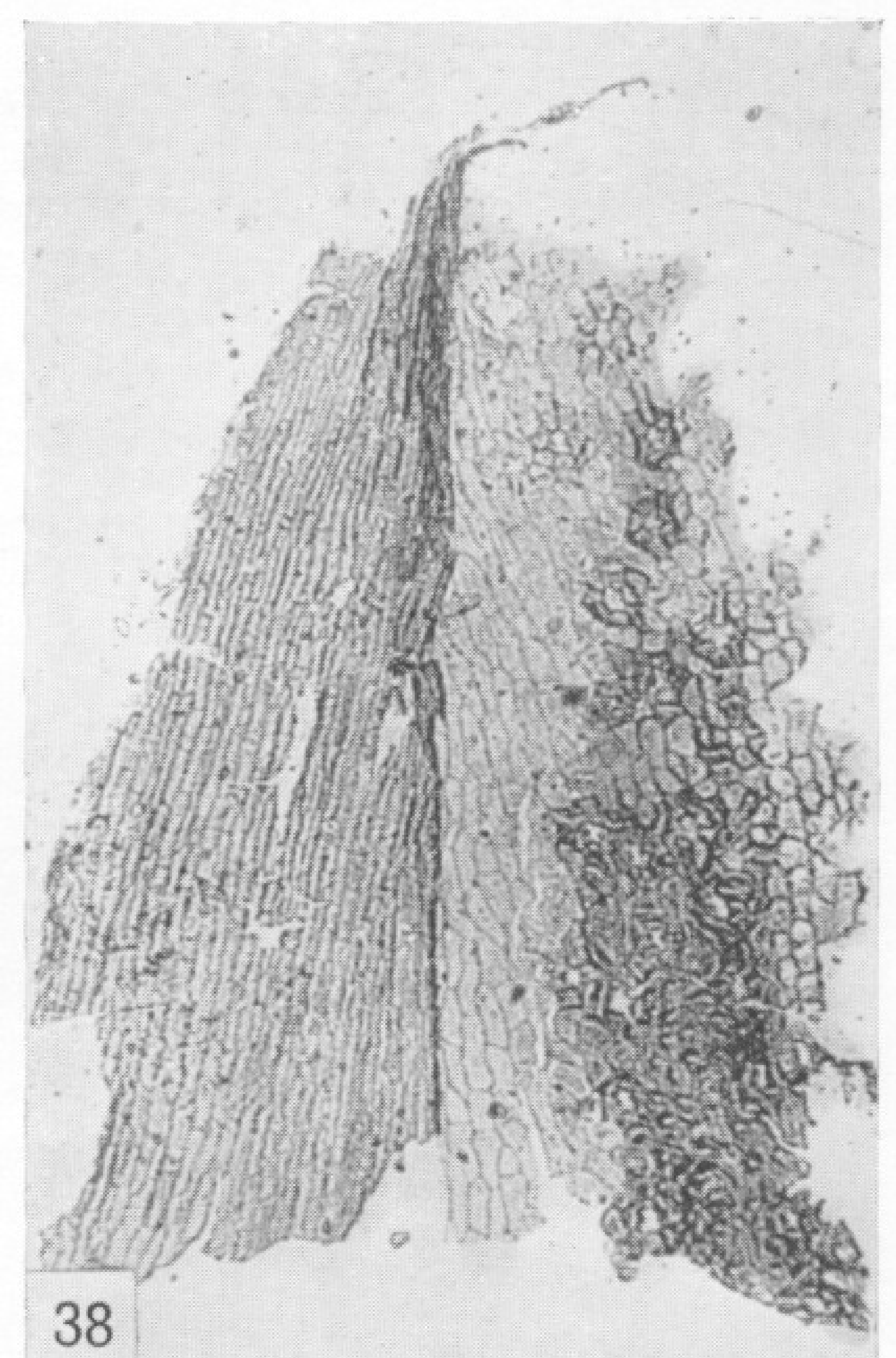

33

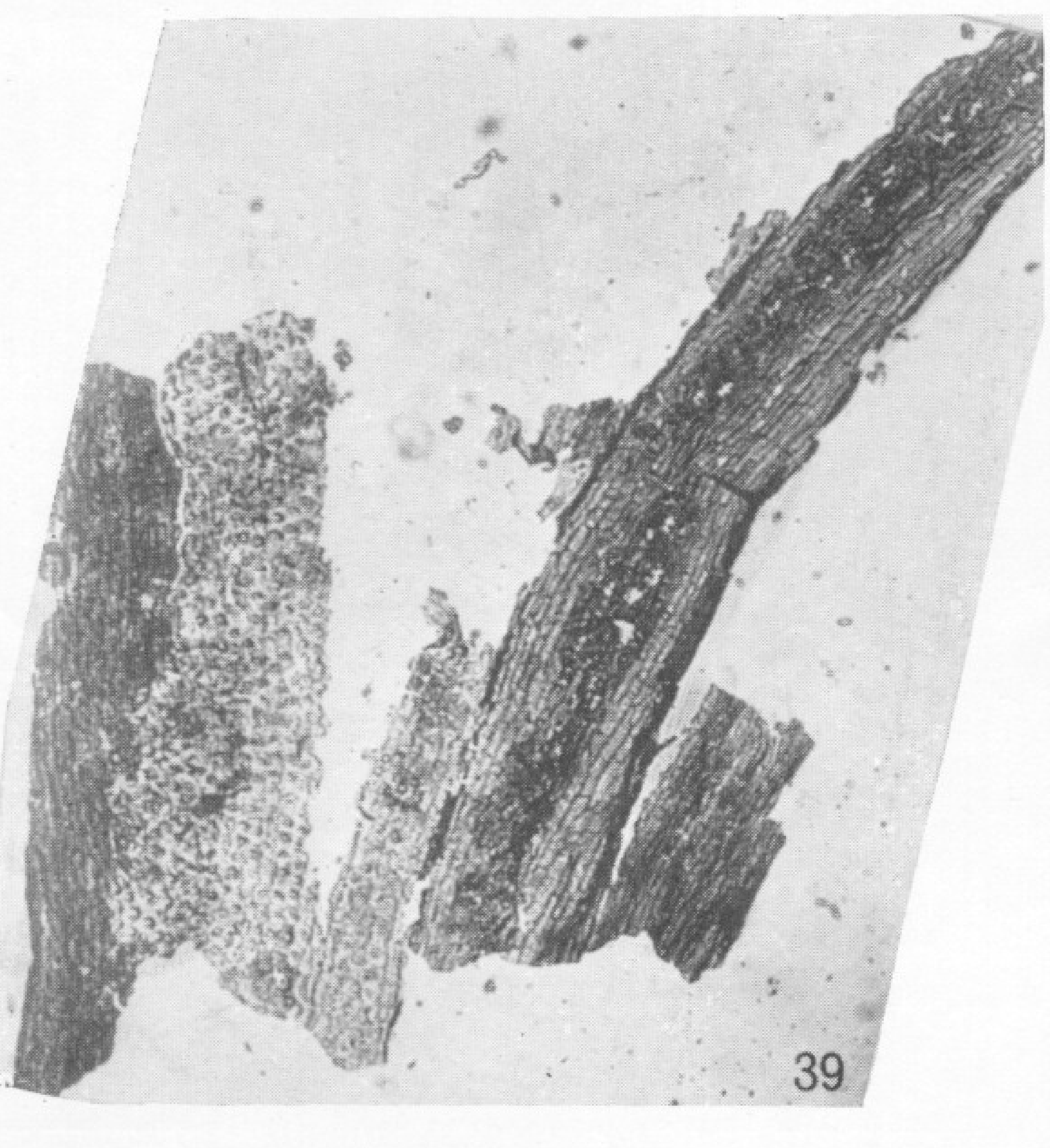

34

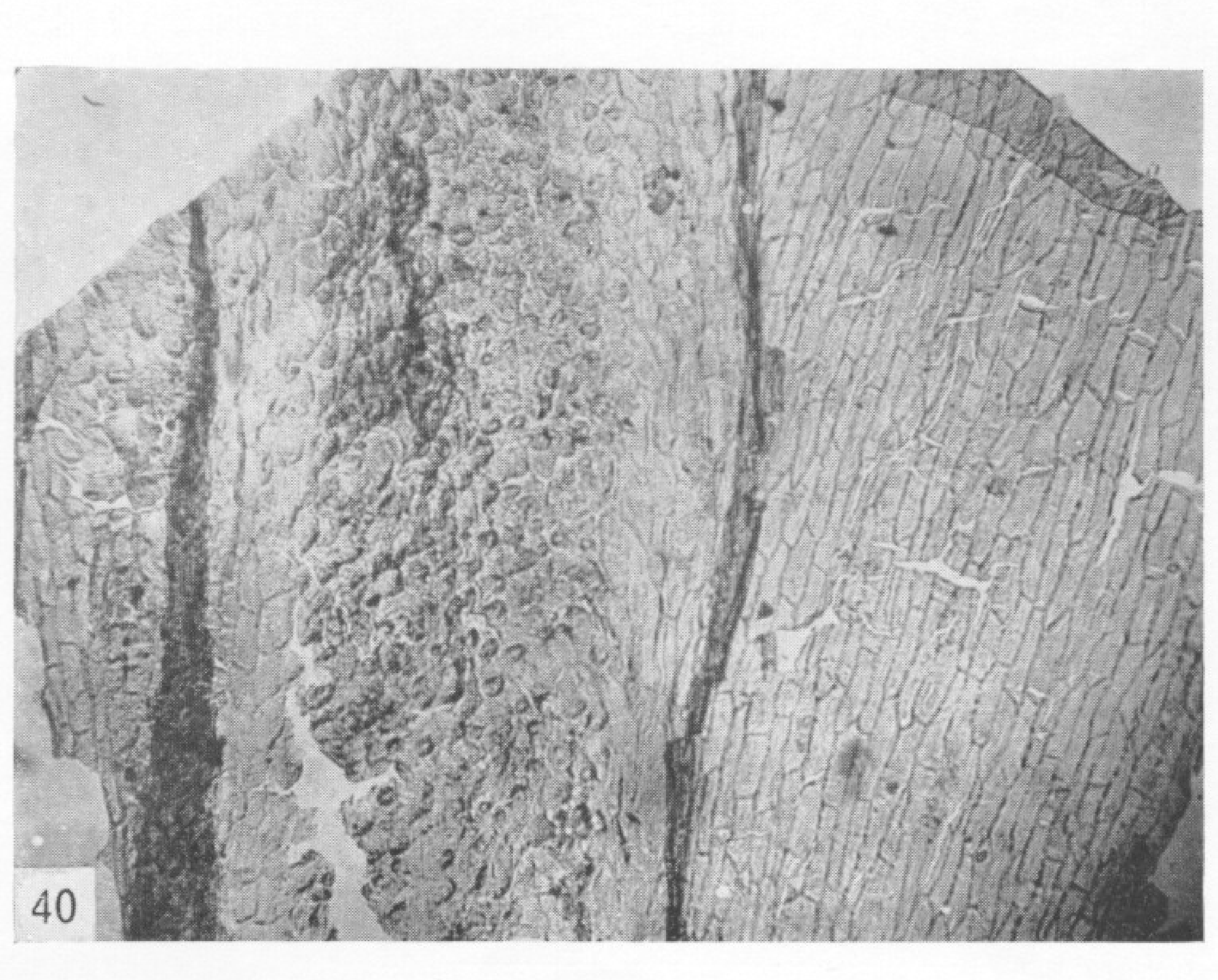

35

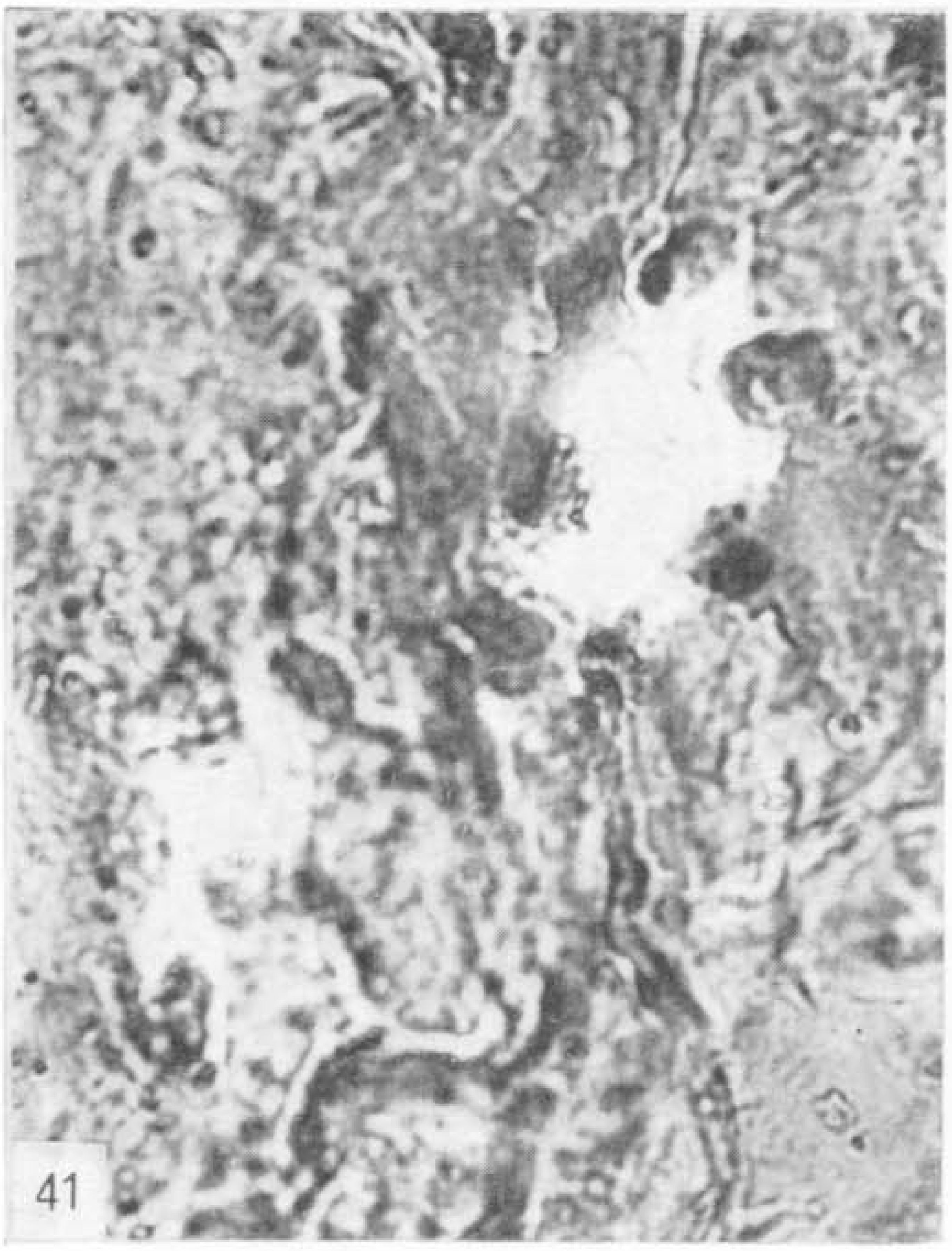

36


37

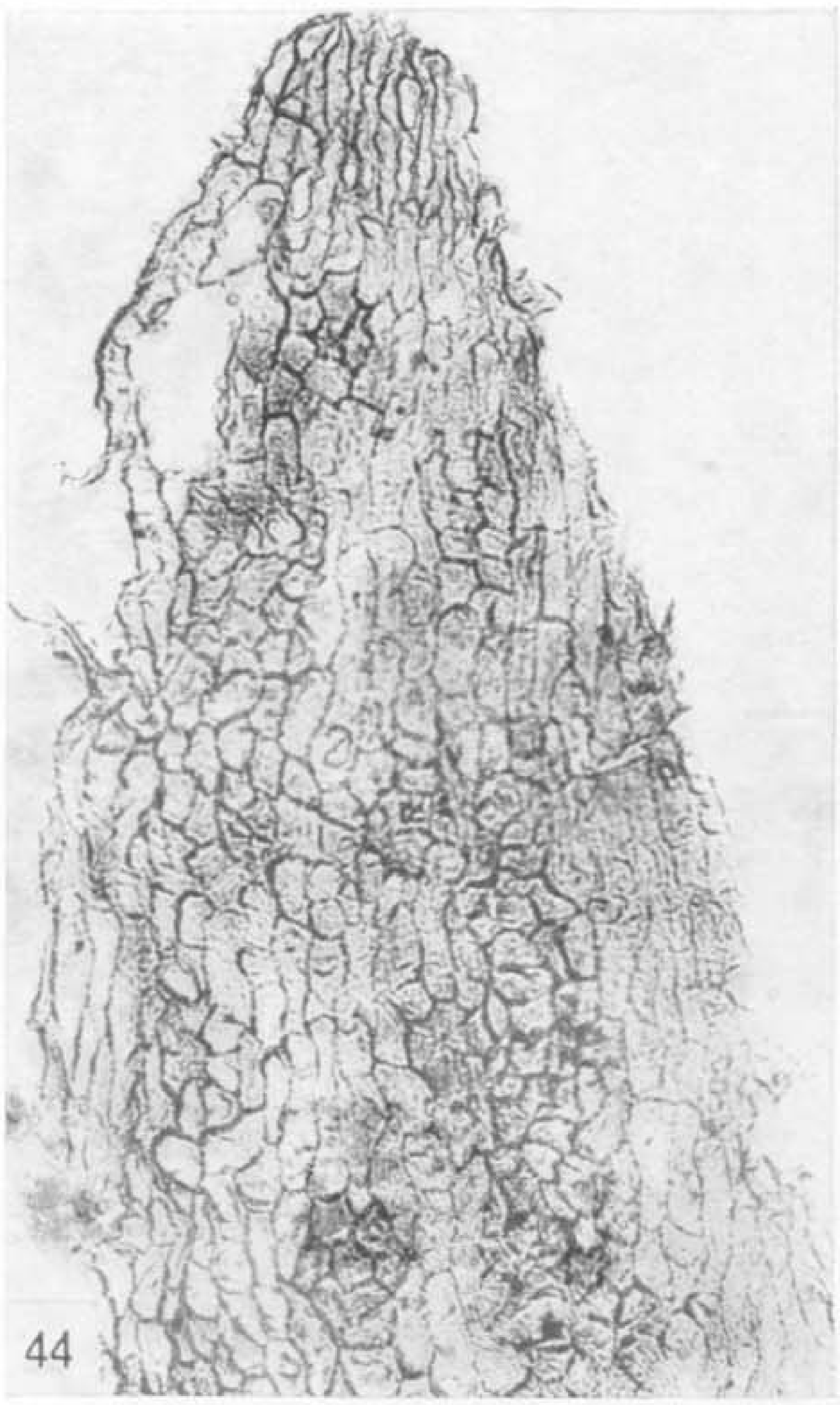
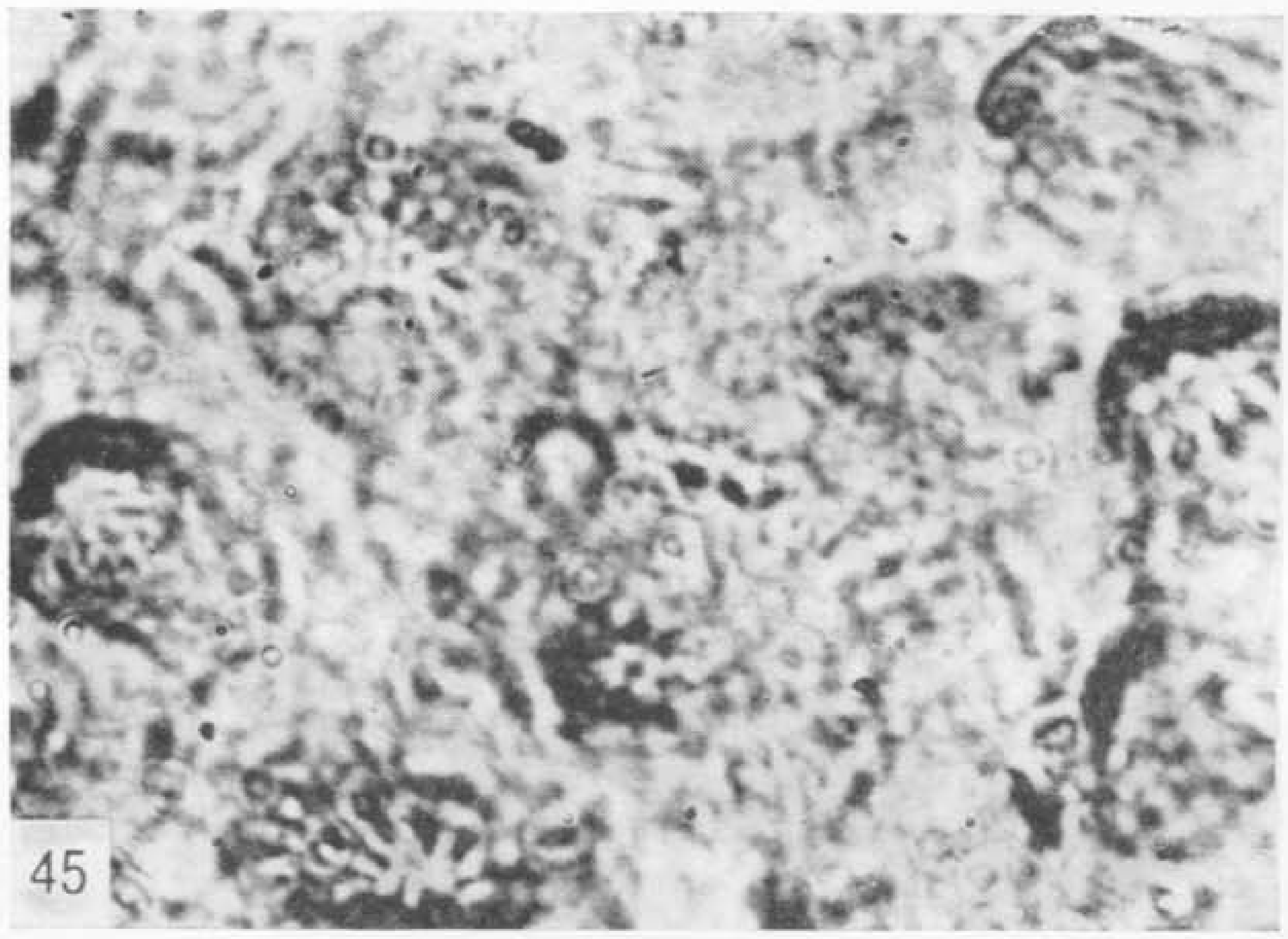

38


39

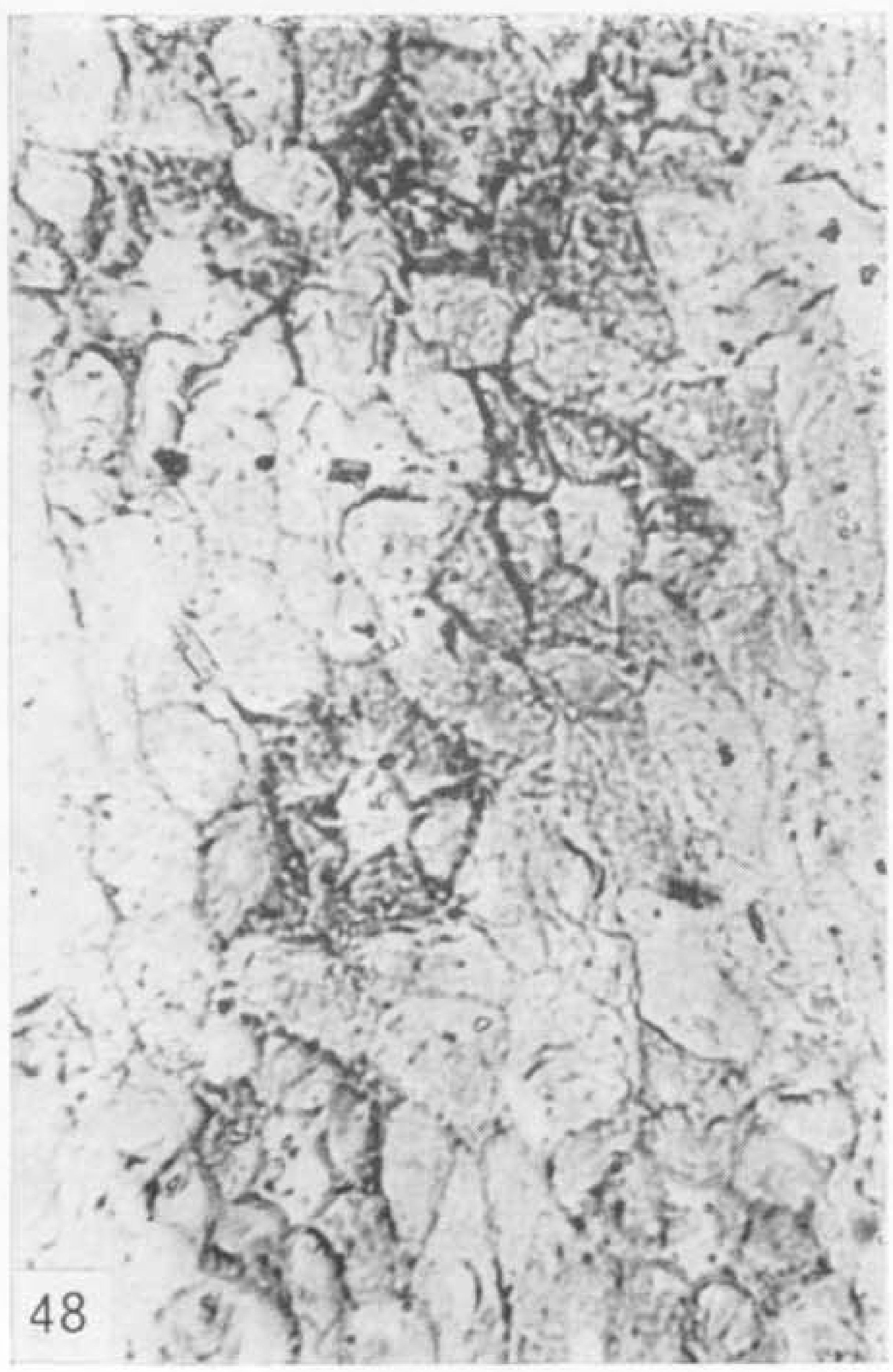

40


41

42

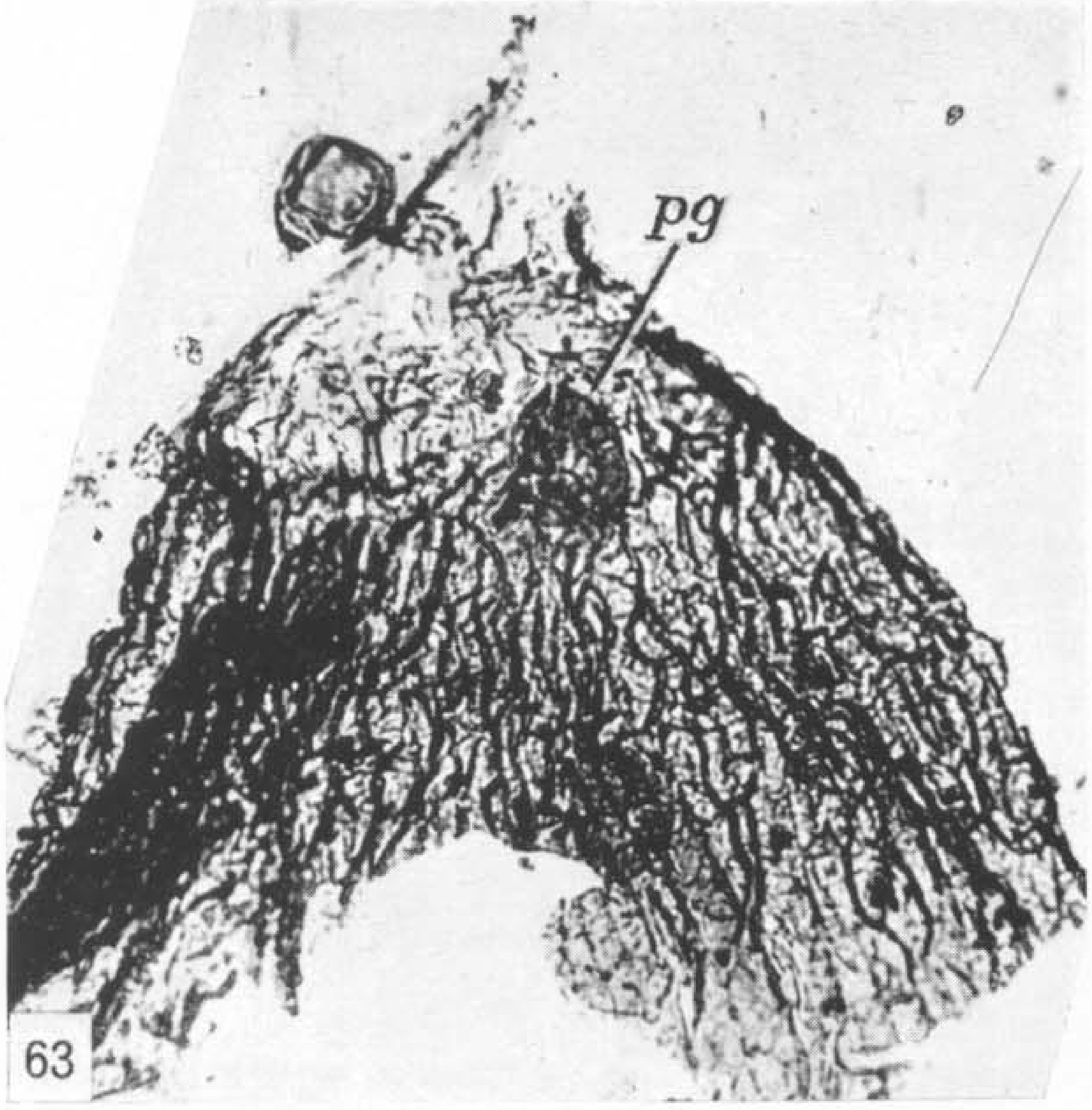
43

44

45

46

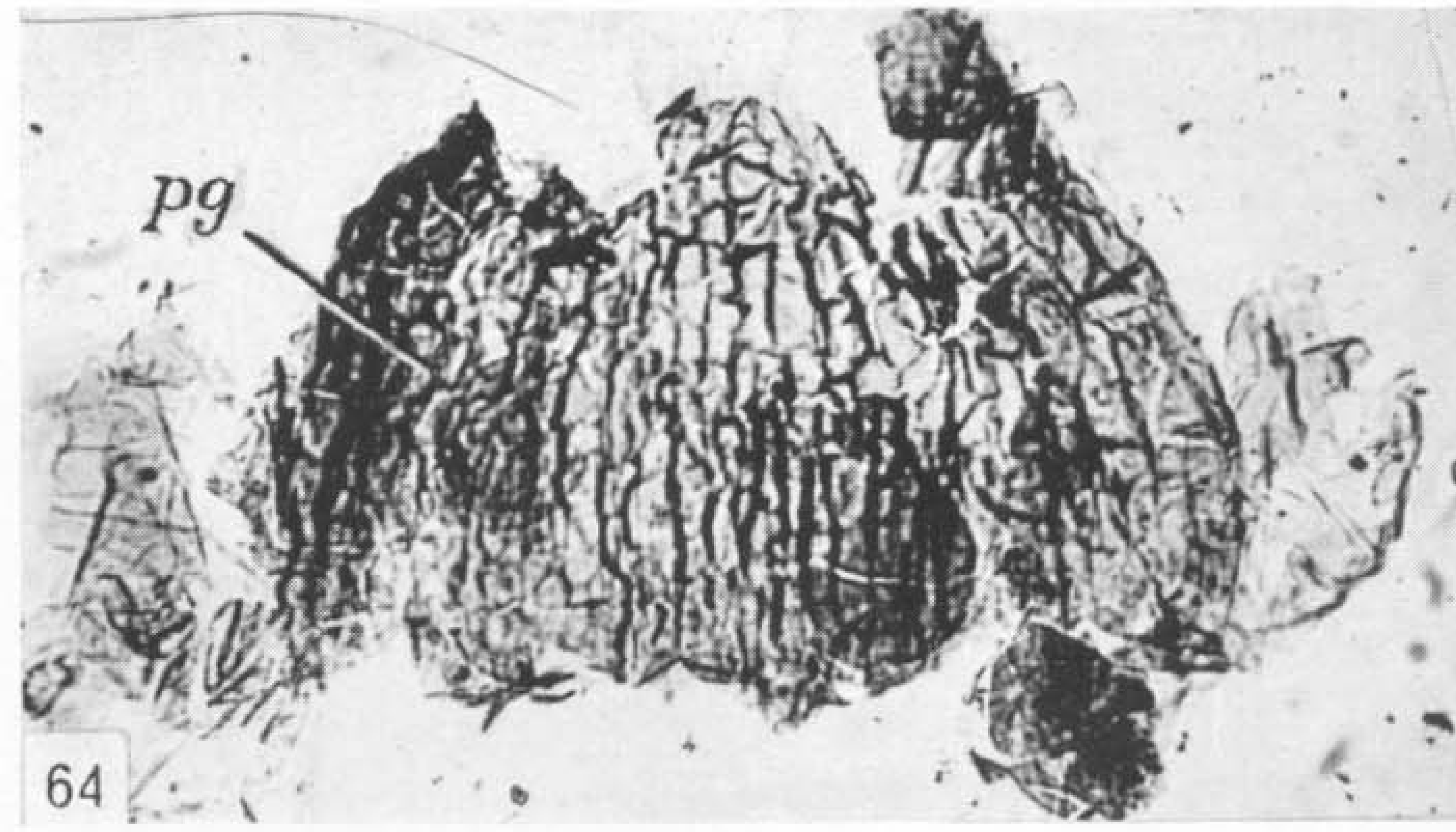
47

48

49

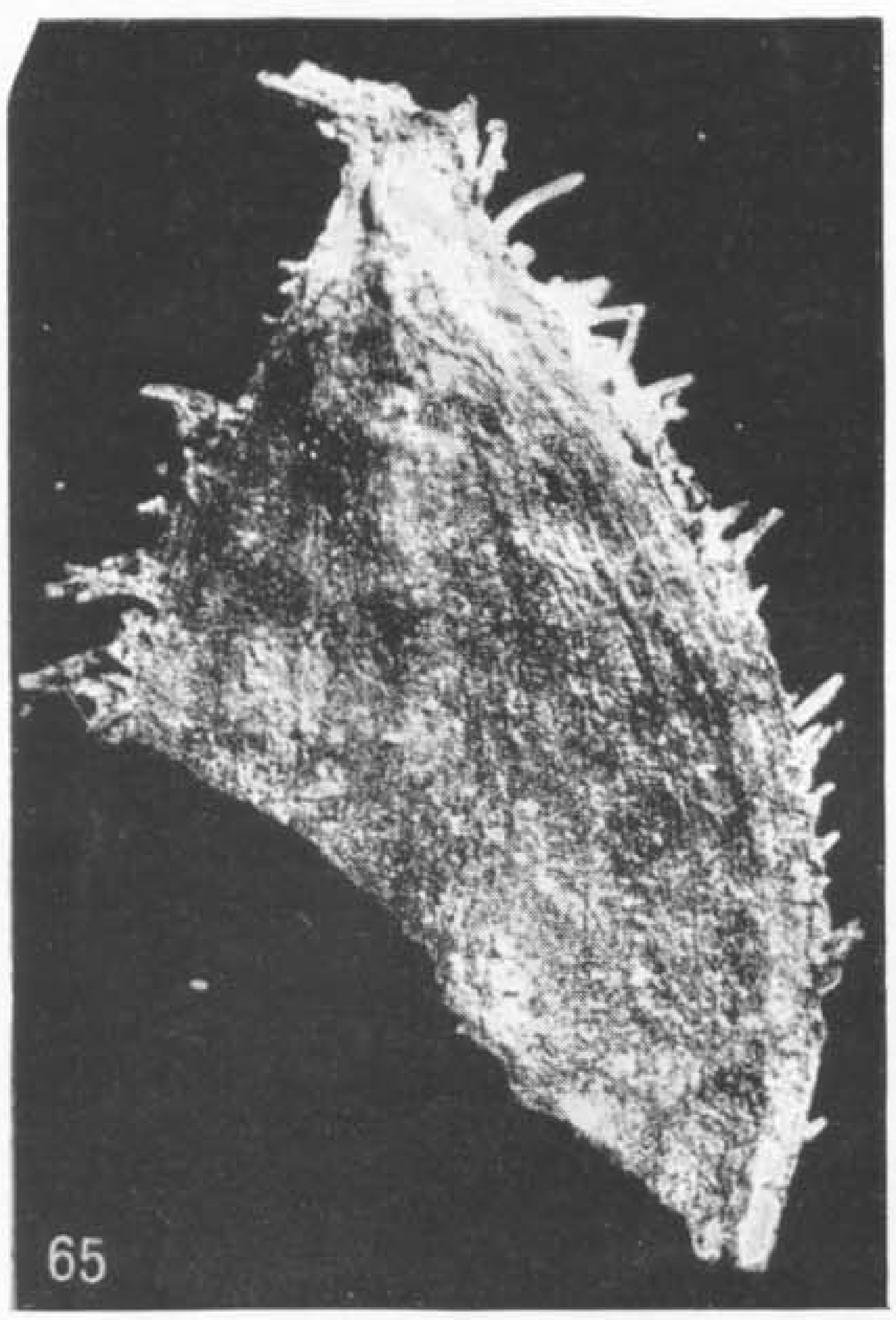

50
51
52
53
54
55
56
57
58
59
60
61
62

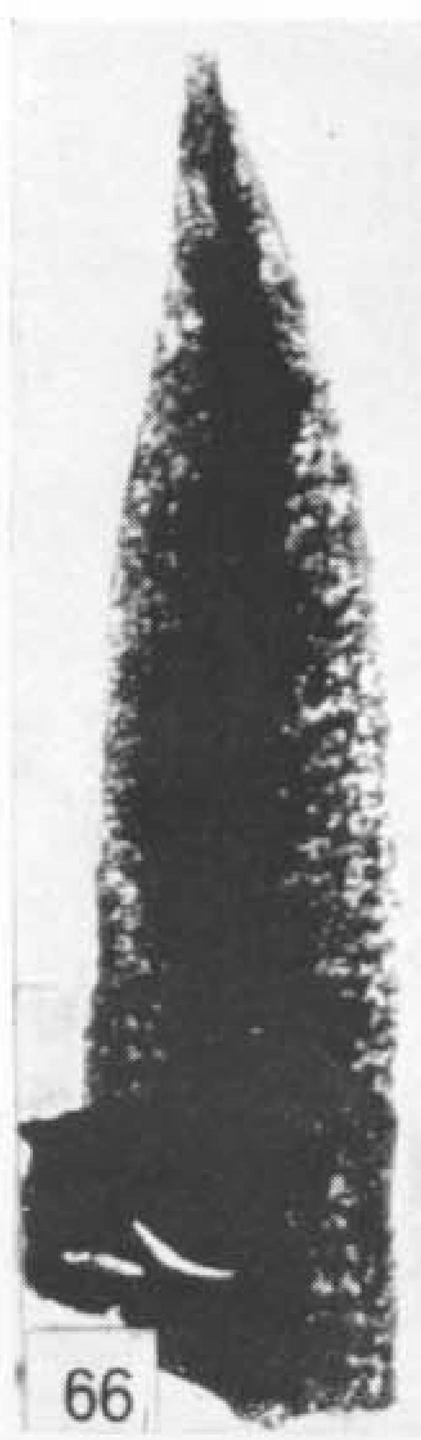


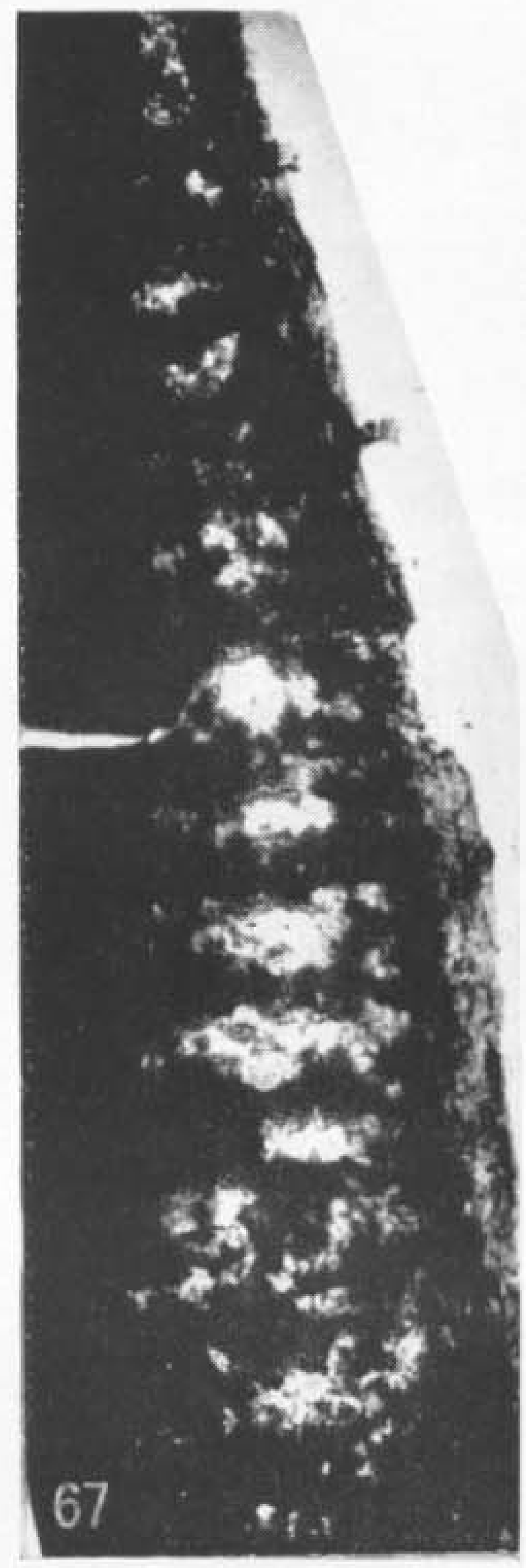
63



64


65

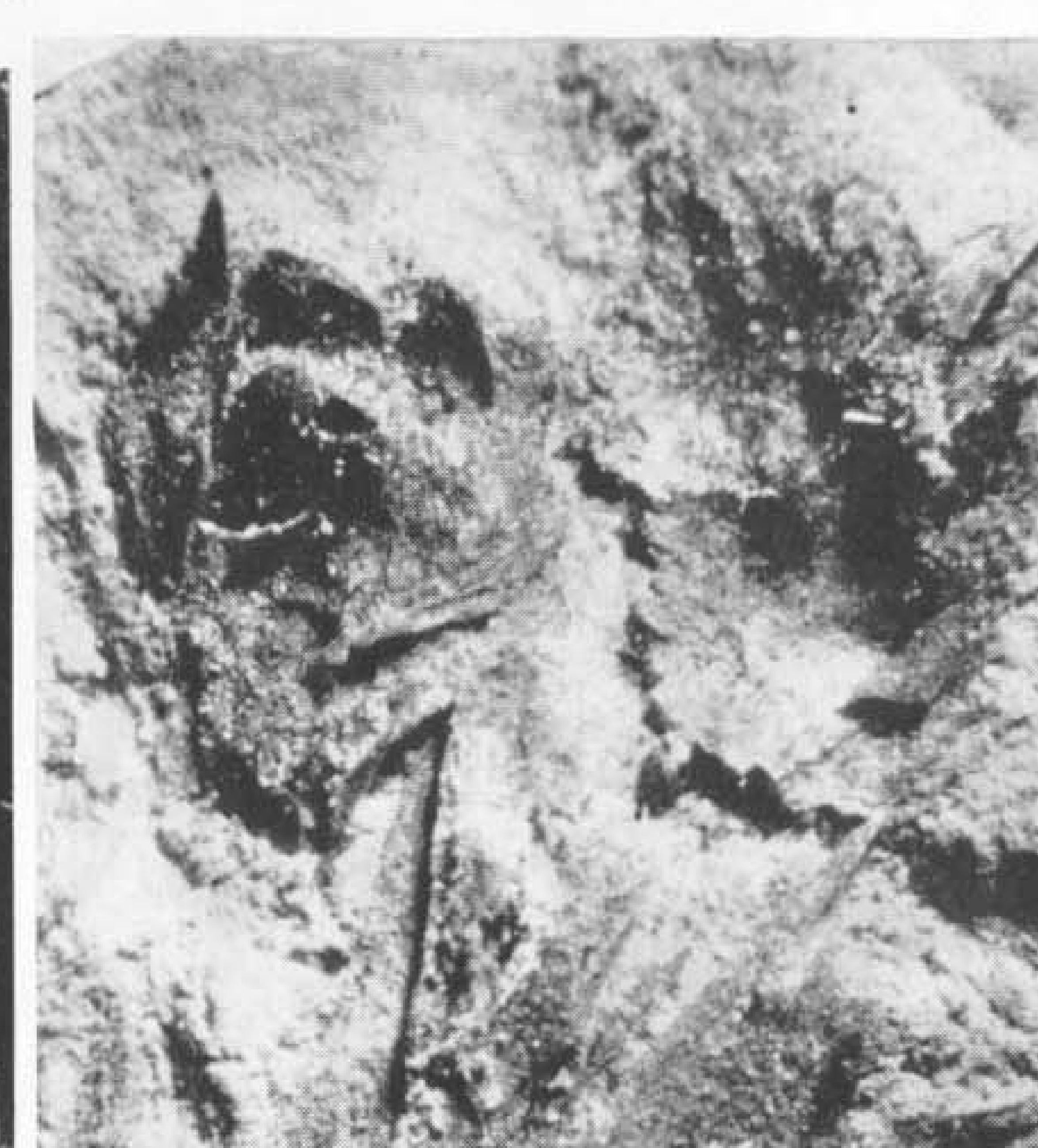

66


67

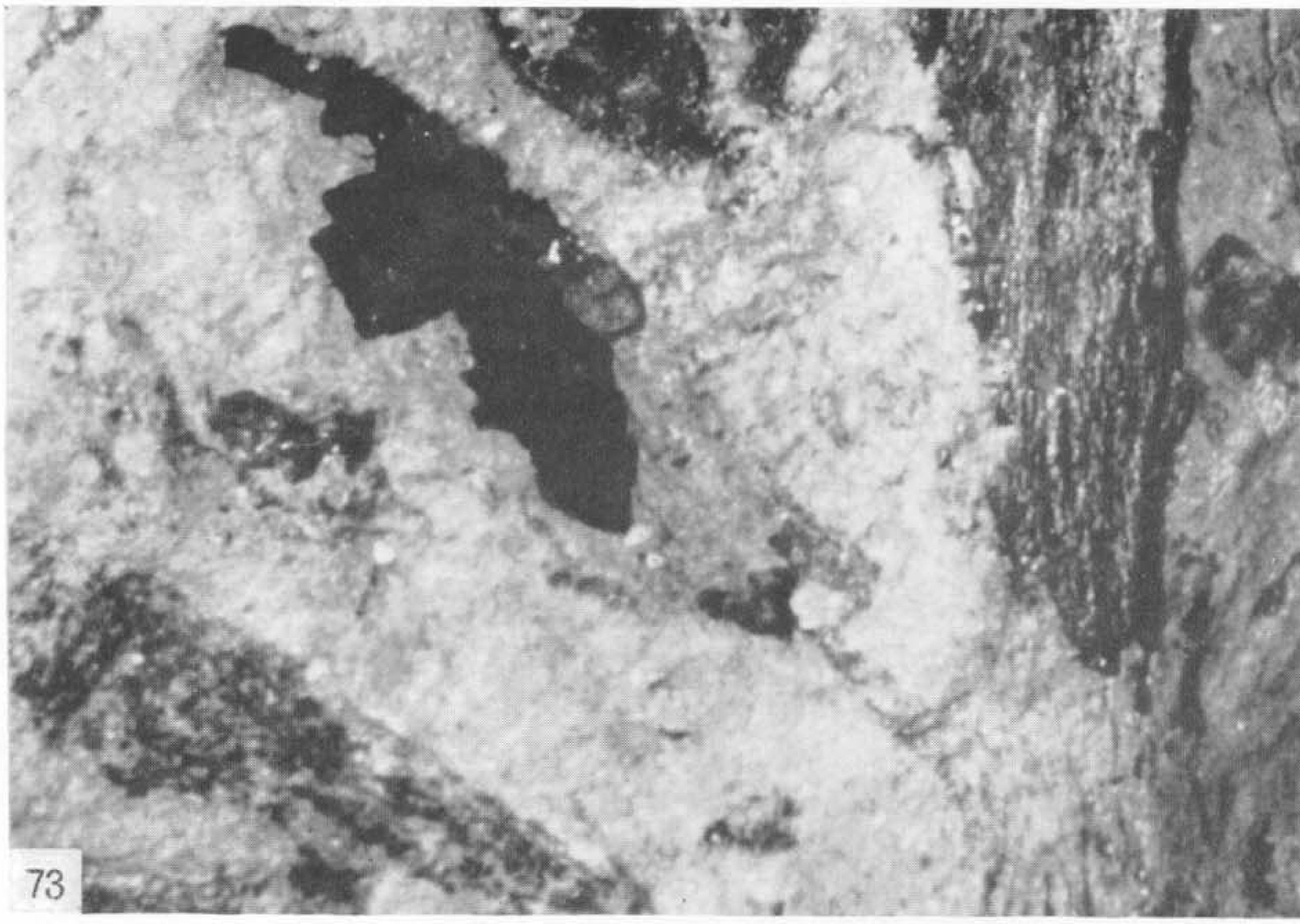

68


69

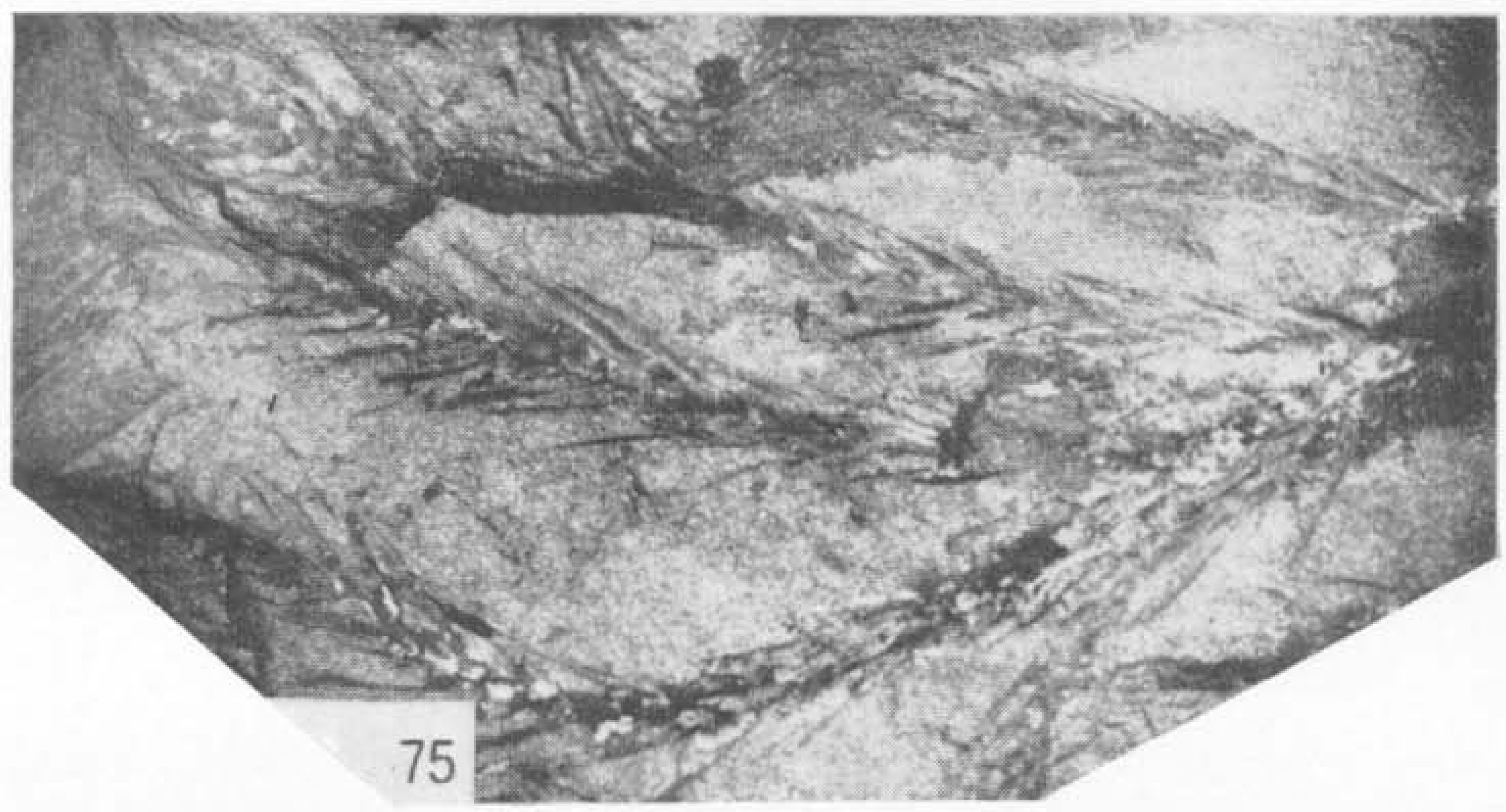

70


71


72

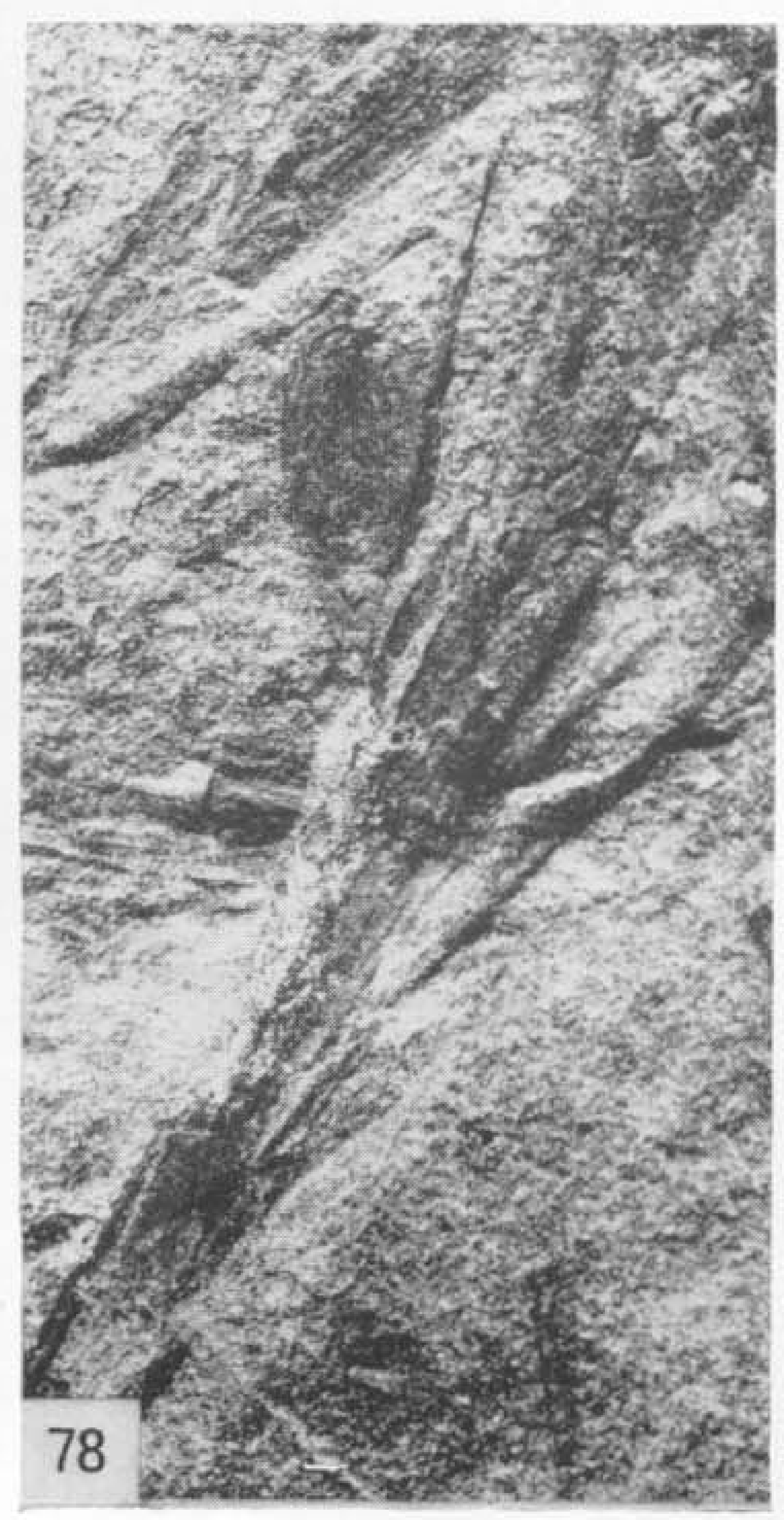

73


74


75


76


77


78