WEICHSELIA RETICULATA

(STOKES ET WEBB) FONTAINE

FROM

THE WEALDEN OF BELGIUM

INTRODUCTION.

The four previous memoirs in this series on the Belgian Wealden flora (HARRIS, 1953; ALVIN, 1953, 1956, 1960) have been devoted to the Coniferales. The subject of the present contribution is one component of the fern flora.

The fossil plant remains which these papers describe were collected by Charles BOMMER at about the beginning of the century and form part of the collection of the Institut Royal des Sciences Naturelles de Belgique in Brussels.

Preliminary work on this fine collection of Wealden plants was undertaken by BOMMER himself, but he published only one short note giving a brief preliminary account of *Weichselia* (BOMMER, 1911). It is not surprising that this single publication should have been devoted to one of the most striking and interesting components of the flora.

The more important of earlier contributions to our knowledge of the flora were those of SEWARD (1900) who described the plants found in the same deposit as the famous Iguanodons at Bernissart, and COEMANS (1866) who described a number of Pinaceous cones, since extensively revised (ALVIN, *loc. cit.*), and some presumed cycad remains from La Louvière.

Spores and pollen have been described by DELCOURT and SPRUMONT (1955) and DELCOURT, DETTMANN and HUGHES (1963).

MATERIAL AND METHODS.

Like all the macrofossil plant remains in the flora, those described here are preserved as lignite without mineralisation. I imagine that the unconsolidated matrix of clay or fine sand was removed simply by washing.

The degree of compression varies : unfortunately, the material from the Bernissart locality from which almost all the remains described in the present memoir come, are generally more severely compressed than most specimens from other localities. Probably for this reason the material does not respond so well to the softening technique which gives such excellent results with the less consolidated material. Swelling may be induced with alcoholic solutions of potash, but larger pieces of material nearly always break up, often into useless fragments. There is also no doubt that, apart from this difficulty of causing the material to swell successfully, the preservation of the tissues is often extremely poor in marked contrast to much of the coniferous material described in earlier memoirs. It has, therefore, not been possible to describe the anatomical structure in the same degree of detail as was possible with the material described earlier.

However, some useful sections of larger specimens have been prepared by a straightforward grinding and sawing procedure. A flat surface is obtained by grinding on a glass plate with fine carborundum powder moistened with paraffin oil (kerosene). After sticking the surface to a slide with fused balsam, a thick section is sawn off and ground down with carborundum moistened with water. (The use of water at this stage causes no damage to the material which is evidently effectively held by the adhering balsam and slide.) When ground thin enough for microscopical study, the section is covered with glycerine-jelly and a coverslip.

Leaf cuticles have been prepared by the same method as before (ALVIN, 1960). Briefly, this method consists in sticking suitable fragments to cellulose acetate film and then macerating gently in alkali followed by hydrogen peroxide and soda.

DESCRIPTION OF MATERIAL

1. THE STEM.

a) MORPHOLOGY.

Three specimens representing pieces of stems are shown on plate 1, figures 1, 2 and plate 2, figure 1. Several other less informative fragments are present in the collection. The stem, judging from the specimens I have seen, was some 5-8 cm in diameter but BOMMER in manuscript notes stated that it was up to 15 cm in diameter. It evidently had an irregular contour due to the rather close, probably spirally arranged, massive petiole bases, and also to the presence of a different kind of organ orientated in the opposite direction to the petioles. This second kind of appendage is assumed to have been some sort of rooting or root-bearing organ; but in its massive structure, it is quite unlike the root in any known fern.

The specimen in figure 1, plate 1 has a total length of about 13 cm and shows evidence of three leaf-bases and two rooting organs. As shown in figure 1 A, it is orientated with the distal end to the top of the photograph; in figure 1 B, the distal end is at the bottom. One petiole is represented by the scar on the right in figure 1 A (a portion of the interal tissues of the leaf base is protruding), another by the scar at the top left (bottom left in figure 1 B), and the third by the scar at the top of figure 1 B. One rooting organ is seen near the bottom in each photograph.

The specimen in figure 1, plate 2 is orientated so that the distal end is to the right in both A and B. It is about 16 cm long and shows evidence of two leaf-bases (the scars at the bottom right in figure 1 A and middle right in figure 1 B). The bases of rooting organs are probably represented by the small protuberance at the top left in figure 1 B, and the large scar seen just left of centre in figure 1 A.

The petiole base was not much smaller in diameter than the stem itself : about 5 cm in these two specimens. It was probably orientated at a rather narrowly acute angle (about 30°) to the stem, so that if the stem was upright, the petioles were sub-erect.

The organs which I suppose to be of a rooting nature were cylindrical, about 2 cm in diameter and orientated obliquely downwards, again making an angle of about 30° with the stem. Nothing is known of their form beyond their extreme base, and the assumption that they had a rooting function is based solely on their orientation. It seems likely that there was one rooting organ associated with each petiole, inserted on the stem obliquely behind the insertion of the petiole. The arrangement is reminiscent of the insertion of the rhizophores at the points of branching of the stem in *Selaginella*.

The specimen in figure 2, plate 1 shows some evidence of a stem dichotomy. The two portions into which the stem appears to be dividing are separated by a deep furrow. No furrow is associated with the departure of a petiole. It is possible, however, that the appearance is due to distortion of the base of a large petiole.

The whole surface of the stem as well as that of the petioles and rooting organs is markedly rugose. The small tubercles giving this roughness are extensions of the superficial sclerenchymatous tissue. It is possible that they represent much modified hairs or ramenta or the persistent bases of such appendages, the upper part of which may have been either caducous or else lost in the course of preservation. The rugosity exhibits no particular pattern and there is much variation in the size and density of the tubercles even on one and the same organ (Pl. 1, fig. 1). The tubercles resemble the thickened hair-bases found on the stems and petioles in a number of living ferns.

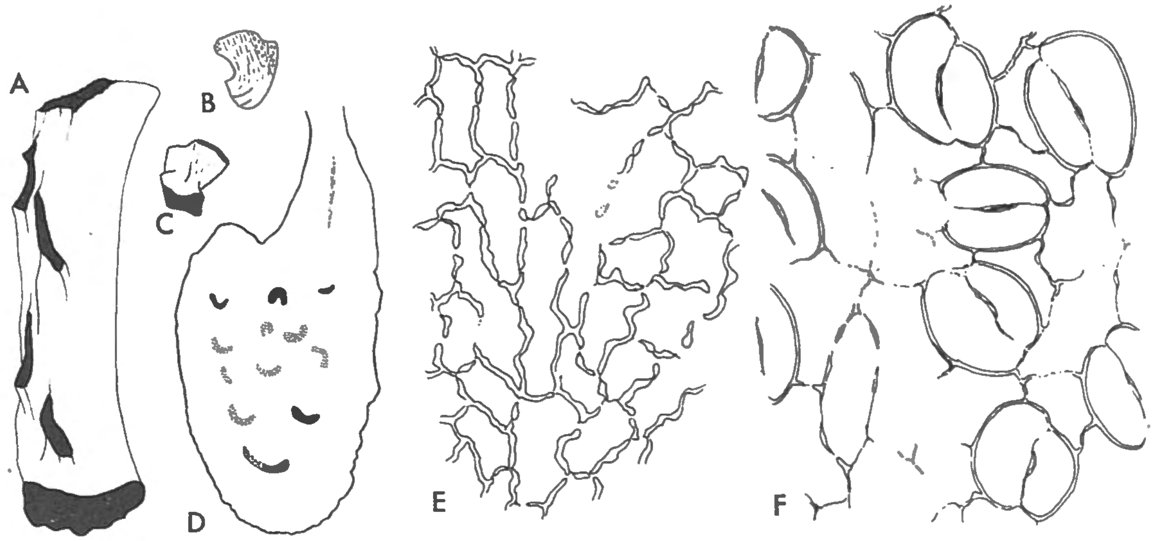

Fig. 1. — *Weichselia reticulata* (Stokes et Webb) Fontaine.
A : secondary vegetative rachis from specimen shown on Pl. 5, fig. 5; acroscopic side. No. 1400. ×9. B and C : portion of the basal pinnule removed from the same pinna rachis. ×9. D : transverse section of a secondary vegetative rachis. (Meristeles shown stippled are only doubtfully distinguishable.) Slide N8/7, section 6. ×20. E : cell outlines from the upper cuticle of the pinnule. Slide N17. ×350. F : lower cuticle. Slide N18. ×350.

Other surface features of at least two kinds also occur on the stem. Small, often distinctly raised, crater-like marks, circular or somewhat elliptical in shape, 2-4 mm in diameter, are of sporadic occurrence. Several are visible on the piece of presumed stem shown in figure 2, plate 2. A second kind of structure, of much greater size (Pl. 5, fig. 1 and 2; Pl. 2, fig. 1 A), is elliptical in shape, 10-15 mm wide and about 25 mm long, orientated with its long axis in the longitudinal direction (Pl. 2, fig. 1 A). Typically these large elliptical « scars » have a somewhat hollowed peripheral zone and a central « hub » which is usually slightly raised. The peripheral region may be smooth (Pl. 5, fig. 2) or bear radiating striations (Pl. 5, fig. 1) sometimes together with small tubercles like those of the general stem surface (Pl. 2, fig. 1 A). The « hub » is typically coarsely granular, but the granulations are different from the normal tubercles. Specimens are too fragmentary to demonstrate whether these « scars » are distributed in any sort of regular order. In the specimen shown in figure 1 A, plate 2, there are two small crater-like marks associated with one elliptical « scar », but there was probably no constant association between the two.

Attempts have been made to obtain sections through these structures, but without success. They appear not to be « scars » in the sense of representing areas where some kind of organ or appendage was attached. It seems more probable that some of them at least represent areas where the surface tissues were modified in connection with aeration of the internal tissues, like the aerophores that occur along the lateral margins of petioles and rachises in many living ferns. Generally in living ferns, the aerophore is a continuous line running along each side of the frond axis, but sometimes, as for example, in some of the Cyatheaceae, the line has become disrupted into short discrete units. The only evidence I have seen that aerophores occurred on the petioles of *Weichselia* is in the decorticated specimen shown in figure 3, plate 3, where there is a « parting » of the striations enclosing an elliptical, slightly depressed area which somewhat resembles the large elliptical « scars » on the stem.

It seems likely therefore that these elliptical « scars » were aerophores, and that they were present on the stem and occasionally along the sides of the petioles. It is conceivable that the small crater-like structures may represent some kind of lesion produced by an external agent during the course of growth.

b) ANATOMY.

Attempts were made to obtain sections from a number of stem fragments, but only one (specimen no. 1580) gave reasonably satisfactory results. (This specimen, incidentally, shows evidence that BOMMER himself may have used it for anatomical study.)

The stem anatomy resembles in a general way that of *Paradoxopteris* HIRMER, 1927, described originally by HIRMER (1925) and later in greater detail by EDWARDS (1933) and KOENIGUER (1966). The Belgian *Weichselia* stem material does, however, show certain structural differences from *Paradoxopteris*. I shall therefore give as detailed an account as the preservation of the material allows and reserve comparison for the general discussion.

The stem consists basically of a peripheral fibrous zone about 1.5 mm thick surrounding a parenchymatous ground tissue containing a polycyclic system of meristeles.

The peripheral zone. — The surface is markedly irregular due to the presence of the tubercles referred to above which give the rugosity characteristic of all the major organs. The tubercles show no special anatomical structure, but are merely extensions of the massive fibrous tissue. No definite epidermis can be recognized in any of the sections I have examined.

The peripheral zone contains a ring of conspicuous cavities or canals some of which may be up to 1 mm in diameter. There is a general tendency for some much smaller ones to alternate with members of the main series. These structures and similar ones found throughout the plant are interpreted as secretory (perhaps gum or mucilage) canals.

The cells of the fibrous tissue (Pl. 8, fig. 3) are somewhat smaller towards the outside than towards the internal ground tissue where the one tissue tends to grade into the other. The outer cells are of the order of 15-20 μ in diameter, the inner, 30-40 μ. They are frequently filled with an opaque substance which in thin sections is reddish in colour. This may represent a natural tannin deposit such as occurs commonly in similar tissues in living ferns.

The stelic zone. — The ground parenchyma in which the meristeles lie is probably more or less homogenous except for the presence of secretory ducts and the fibrous sheath tissues associated with the meristeles.

The meristeles lie in concentric rings. The section in plate 8, figure 1 represents a portion only 1.2 cm thick and contains 5 rows of meristeles (portions of the 5 outermost rings). In a stem 10 cm in diameter there could have been 20 or more meristele rings, for the successive rings tend to become closer together towards the interior.

Members of the outermost ring of meristeles lie on radii regularly alternating with those on which the large secretory canals of the peripheral zone lie. Similarly, the meristeles of the inner rings alternate with secretory canals lying in the ground parenchyma between the rings. Other possible secretory canals appear sometimes to run adjacent to the meristeles on the centripetal, concave side (Pl. 8, fig. 2), though these, due to the usually poor cellular preservation, are often indistinct, and may indeed only represent areas where the tissues have broken down due perhaps to differential shrinkage at some stage.

Each meristele has fibrous tissue associated with it in the form of a more or less continuous but uneven sheath which is always much thicker on the centripetal side. Only the outermost meristeles lack fibrous tissue on their outer side, though here the ground parenchyma is somewhat smaller-celled and slightly thicker-walled than that further in; it also quickly grades into the peripheral fibrous tissue outwards. The centripetal fibrous sheath tissue is thickest in the outermost ring (1 mm) and decreases in thickness in successive inner rings (about 0.5 mm in the 5th ring). The outer (centrifugal) fibrous sheath tissue which begins in the 2nd ring (where it is a little less than 0.5 mm) also decreases in the inner rings. The sheath appears to become very thin or even discontinuous at the sides of the meristeles.

The vascular tissues are not well preserved in any of the sections which I have been able to prepare. One of the best bundles is that shown in figure 2, plate 8. The meristele is apparently concentric. No endodermis can be definitely recognized, though from the sharp definition of the inner limit of the sheath tissues I would guess by analogy with living ferns that one was present. The xylem mass is not uniform in thickness, but is thinnest in the middle and thickest near the ends of the « C ». It appears to consist mainly or wholly of tracheids, some of which are very large, frequently 100 μ in diameter, sometimes up to 130 μ. The largest elements lie near the ends of the curved mass.

In none of the stem sections do any of the meristeles show any clear evidence of division or anastomosis. Only in one or two bundles may a small strand be in the process of separating off from the ends of one of the large meristeles. This is indicated mainly by the contour of the outer limit of the centripetal sheath tissue. Some lateral coalescence of meristeles may occur nearer the centre of the stem, but unfortunately no satisfactory sections have been obtained from this region.

2. THE VEGETATIVE FROND.

a) MORPHOLOGY.

Frond remains are represented by a large and bewildering array of petioles, pedate organs, rachises of several kinds and both attached and detached laminate pinnules. Plates 3-6 show something of the range of these remains.

The identification of all these fragments as one kind of plant was at first not at all obvious; it has been deduced from various evidence. Of special importance has been (1) the characteristic rugosity of the surface of all the more massive organs, (2) the occasional attachment of one kind of organ to another, and (3) anatomical evidence.

One puzzling feature about the frond, judging from specimens representing the more proximal portions, especially petioles, is the amazing variation in size. (There is considerably less variation in the ultimate rachises and laminate pinnules.) It is well known that all ferns begin life as diminutive juvenile forms, and in general, the larger and more complex the characteristic adult form, the more slowly the full adult size is attained. Thus, in a population there is likely to be a proportion of juvenile individuals, and this proportion might be greater the more massive and complex the adult form of the species. The range of variation in size of petioles and rachises amongst these remains of *Weichselia* is probably no greater than that represented by the difference between a sporeling and a full-sized adult of a present-day fern like *Angiopteris evecta*.

A reconstruction of the plant including one vegetative frond is shown in text-figure 3. The primary divisions of the frond, which I am calling the primary pinnae, were borne in a palmate fashion at the end of the petiole. The primary pinnae were themselves twice pinnate. I am calling their main divisions the secondary pinnae and the ultimate laminate segments will continue to be called pinnules, as in the past.

The petiole. — Portions of petioles, some with the pedate terminal part attached, are shown on plate 3 and plate 4, figures 3-6. (Those on plate 3 are natural size; those on plate 4 are twice natural size.) The petiole varies from 0.2-5.0 cm in diameter. All specimens except the two smallest (Pl. 4, fig. 3 and 4) show the characteristic rugose surface, though there is variation in the degree and coarsenecs of the rugosity; the smaller specimens are smoother than the larger.

All specimens are compressed. They were probably originally round or elliptical in transverse section, with the long axis of the ellipse lying vertically. There is no convincing evidence that an adaxial groove was present, except just below the pedate head. The adaxial side may, however, have been somewhat broader and flatter than the abaxial (Pl. 3, fig. 2). The large specimen shown in figure 1, plate 3 has irregular grooves along both edges, but these are probably the result of severe compression which has produced wrinkling of the dense peripheral fibrous tissue.

The flattened distal face of the pedate head is not always orientated at right angles to the petiole. In the larger specimens it is turned so that this face (the morphologically adaxial side) is orientated somewhat abaxially. The largest pedate head (Pl. 4, fig. 1) was probably set at about 120° to its petiole, so that if the petiole was inclined at 30° to the vertical, the head was also inclined at 30° to the vertical. In the smaller specimens the head is more nearly at right angles to the petiole (Pl. 4, fig. 4 and 6), and in the two smallest (Pl. 4, fig. 3 and 4) the distal (adaxial) side was not turned quite at right angles and was therefore still orientated adaxially. This perhaps accords with the view that the smaller specimens represent more juvenile states.

The pedate head is divided peripherally into up to 15 segments; these are interpreted as the bases of the primary pinnae. Again there is variation in number with the size of the specimen. Thus, the largest (Pl. 4, fig. 1) had about 15 primary pinnae, whereas those shown on plate 3, figures 4-6 had about 10-12, and those on plate 4, figures 5 and 6, about 8 or 9. The primary pinna bases are not all the same size in a given specimen, nor are they orientated quite strictly radially in relation to the centre of the head. There is always a markedly deep and wide sulcus at the position of the adaxial groove (indicated on plate 3 by arrows). The pinna bases adjacent to the sulcus are usually larger than the others (Pl. 3, fig. 4-6), but there is sometimes an indication that they may have subdivided (e.g., Pl. 3, fig. 6 B).

The pedate organ may be compared with the end of the petiole in the living fern *Matonia pectinata* where it divides up into the palmately arranged pinnae. Plate 4, figure 2 shows the adaxial side of this portion of a frond of *Matonia*. By comparison with the pedate organ shown in figure 1, it is possible to see how the latter may have been derived. The massive, solid structure in *Weichselia* has probably resulted from some contraction and fusion of the bases of the primary pinnae. One feature of the *Weichselia* organ, however, which does not completely accord with this interpretation, is the large size of the pinna bases immediately adjacent to the adaxial sulcus, for these correspond in position to the smallest pinnae in *Matonia* (i.e., the morphologically most distal pinnae). A possible explanation is that these large, most adaxial segments in *Weichselia* do not represent single pinnae but would divide up into a number of successively smaller ones more distally beyond the point where they have broken off in the specimens. They would thus represent not merely the most distal (smallest) pinnae in *Matonia*, but rather two or more of the most distal ones.

The primary pinna. — On plate 5,figures 3-10 are shown several rachises interpreted as portions of primary pinnae. All consist of a relatively stout main axis bearing two rows of slender laterials often represented only by short, stub-like bases. The rachises vary in breadth greatly (0.2-2.3 cm), their laterals much less (0.7-2.0 mm).

The identification of these rachises as belonging to the same plant as the stems and petioles rests on their fine surface characters and their anatomy. Their identity as portions of vegetative frond of *Weichselia* is based on the actual attachment, in one single instance, of a clearly recognizable fragment of a laminate pinnule, and also again on anatomy. The single attached pinnule fragment was found on the secondary rachis indicated by an arrow in figure 5, plate 5. A drawing of this is shown in text-figure 1 A. The secondary rachis (text-figure 1 A) shows several pinnule scars which agree in shape, position and arrangement with those of typical detached secondary pinnae (many of which are illustrated on plate 6). The fragment of pinnule (text-figure 1, B and C) was the basal one on the rachis; it is rather auricle-like and shows the base of the thick midrib and a portion of the lamina with veins and large stomata.

The surface of most of the specimens of primary pinna rachises is striated longitudinally. Similar striation can be seen on the bases of primary pinnae attached to the pedate heads. The larger pinna fragments also show the rugosity characteristic of the stems and larger petioles of the plant. This can be seen clearly in the large specimens on plate 5, figures 9 and 10, where the lower (abaxial) side is both striated and rugose. The rugosity, however, is finer than that of the stems and larger petioles and apparently decreases from the proximal end to the distal region. The specimen on plate 5, figure 10 is considerably smoother at the right hand (distal) end than at the other. All the most slender rachis fragments are only finely striated.

The larger and more proximal portions of rachis tend to be compressed laterally, suggesting that they were probably deeper than broad. Other more slender specimens representing probably mainly median and distal portions are generally compressed in the adaxial-abaxial plane, suggesting that these were relatively broader.

Secondary pinnae apparently did not begin right at the base of the primary pinna rachis. None of the bases attached to pedate organs shows any secondary pinnae. What I take to represent a portion of primary pinna rachis very near the base is shown in figure 3, plate 5. The three scars of secondary pinnae (marked by arrows in figure 3 B) are very weak, but below these there are two or three even weaker ones hardly discernible in the photograph. The outline of the whole primary pinna was therefore probably broadly lanceolate.

No wing-like aphlebial structures like those reported by Lipps (1923) and Daber (1968) have been seen, but in large specimens like those shown in figures 9 and 10, plate 5, the bases of the secondary pinnae are connected by a weak wing-like extension from the side of the main rachis. It is possible that this wing expanded below into the aphebiae observed in the German material.

Secondary pinnae, at least in the more proximal region, are attached to the primary pinna rachis much nearer the adaxial side than the abaxial. This is seen well in the large, laterally compressed specimen on plate 5, figures 9 and 10.

Secondary pinnae vary in their distance apart from 5-7 mm, and often appear to be orientated forwards and upwards. This is similar to the usual orientation of the pinnules on the secondary pinna rachises.

The secondary pinna. — A range of secondary pinnae and pinnules is shown on plate 6. Bommer was of the opinion that these represented a number of different species. I am including them all in one because it seems to me that they could all be within the range of variation of a single species, if not even within that of a single frond.

The secondary pinna rachis is typically deeper (i.e. thicker in the adaxial-abaxial direction) than broad (0.6-2.0 mm deep, 0.5-1.2 mm broad). The pinnules are inserted along the top edge (the adaxial side), so that the bases of the opposite rows of pinnules are separated only by a narrow adaxial groove (Pl. 6, fig. 4 and 6). In many of the specimens, the two opposite rows of pinnules are not lying in one plane, but at an angle; sometimes they are inserted almost vertically and lie in parallel planes (Pl. 6, fig. 2, 3, 10, 11 and 12). This « butterfly » orientation of the pinnules is a well known characteristic of *Weichselia*. In some specimens, the two rows of pinnules do lie more or less in one plane; this is evidently true of the distal portions of pinnae (Pl. 6, fig. 9 and 13).

There is much variation in the size and shape of the pinnules. One which may be taken as a fairly typical example is shown on plate 5, figure 1. It is slightly sigmoid, parallel-sided, except for the rounded end, and the venation is more pronounced on the lower surface (fig. 1 B) than on the upper (fig. 1 A). The midrib fades into the net venation before reaching the apex. There are generally 4-5 meshes between the midrib and the pinnule margin, and the meshes tend to be elongated nearly parallel to the long axis near the midrib, but gradually more transversely near the margins. The two surfaces of the pinnule are markedly different in contour : the upper surface is convex with the midrib marked by a furrow, whereas the lower surface shows the midrib as a broad ridge, and between it and the adaxially rolled margin, the lamina is concave with the venation in rather bold relief. Under a stereoscopic microscope it is possible to see the large apparently bulging stomata in the interstices of the veins (Pl. 7, fig. 1) (*).

Neglecting specimens which obviously represent terminal portions of pinnae (e.g. Pl. 6, fig. 9) where the pinnules are very small and laterally adnate, the pinnules vary in length from 3.0 mm to 6.0 mm (mean 4.3 mm) and in breadth from 1.3 mm to 2.5 mm. The distance apart of successive pinnules on one side of the rachis varies from 1.5 to 3.0 mm (measured from base to base of successive pinnule midribs). Due to these differences in breadth and distance apart, there is considerable variation in the degree to which successive pinnules are separated by spaces or, at the other extreme, overlap. There is no obvious correlation between these differences. Thus, the midribs of successive pinnules in the specimens on plate 6, figures 2, 5 and 7 are the same distance apart, but due to their larger size in figure 2, they overlap, whereas in figure 7 they are separated by wide spaces. In the specimen in figure 6, they are the same breadth as in figure 7, but are closer together.

The base of the pinnule varies from being distinctly constricted on both acroscopic and basiscopic sides (e.g. Pl. 6, fig. 1, 2, 3, 10, 11 and 12) to being either straight (both sides,

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(*) This has now been confirmed by observations on English material using the scanning electron microscope (Alvin, 1970, *Proc. 3rd Annual SEM Symposium*, Chicago, pp. 121-128).

e.g. Pl. 6, fig. 5 and 6) or straight on the acroscopic side and distinctly decurrent on the basiscopic side (e.g. Pl. 6, fig. 4 and 7). I suspect that this varied within individual pinnae, and that in the proximal region the pinnules were more constricted at their bases, but became more parallel-sided or slightly decurrent towards the distal end before eventually becoming joined together at their bases towards the extreme end of the pinna. Certainly the basal pinnule shown in text-figure 1 B and C seems to be extremely constricted, almost shortly stalked, but the second and succeeding pinnules, judging from the shape of their scars (text-fig. 1 A) were probably progressively less constricted.

I envisage a series of specimens such as those shown in figures 2, 6 and 9, plate 6, as representing successively more distal regions of pinnae.

b) ANATOMY.

The petiole. — The structure of the petiole is basically similar to that of the stem. There is a peripheral fibrous zone containing a ring of large secretory canals and an inner region consisting of parenchymatous ground tissue with secretory canals and C-shaped meristeles with associated fibrous sheaths.

The specimen believed to represent a large petiole, shown on plate 3, figure 2, contains about 12 concentric rings of meristeles. The petiole attached to the medium sized pedate head shown on plate 3, figure 6 shows evidence of about 6. The small specimen in figure 6, plate 4, a section of which is shown on plate 9, figure 1, contains 3. The broken petioles of two of the smallest specimens (Pl. 4, fig. 3 and 5) also show evidence of polycycly, each containing 2 or 3 rings. The number of meristele rings is thus related to the size of the petiole.

As in the stem, meristeles alternate more or less regularly with secretory canals in the ground tissue. Again, at least in the large specimens (Pl. 3, fig. 2 B), the meristeles (including their fibrous sheaths) of successive rings decrease in size from the outermost to the innermost, and the rings become closer together.

However, the petiole shows some dorsiventrality in its organisation. Along the abaxial (lower) side, the meristeles tend to be more or less confluent to form long corrugated flanges of vascular tissue. This is well seen at the bottom of the specimen in figure 1, plate 9. This coalescence, however, appears to occur only in the inner rings in larger specimens. Also, again in smaller specimens, the meristele rings are much less regular on the adaxial side.

The meristeles in the petiole show evidence of ramification more frequently than in the stem. Small strands appear to arise from the ends of the main C-shaped strands and run between the rings of main strands in much the same manner as in *Paradoxopteris stromeri*, but they seem to be very irregular in their occurence and distribution. The destiny of these is unknown; they may fuse again into the main series at a different level.

Unfortunately no well preserved meristeles have been observed in any of the sections of petioles. Indeed, so poor is the preservation, that it is often impossible to distinguish between meristeles and secretory canals. As in the stem, there is apparently sometimes present a secretory canal on the inner concave side of the meristele.

The primary pinna. — Like the petiole and the stem, the primary pinna also possesses a polycyclic structure. Indeed, it virtually repeats the structure of the petiole. Again, the number of rings is related to the size of individual specimens. Evidence of about four rings can be seen in some of the attached pinna bases in the medium-sized pedate heads in figures 4 and 6, plate 3, and of about six in the larger specimen in figure 1, plate 4. The detached rachis in figure 4, plate 5 contains about five rings, whilst the small one in figure 7 has two or possibly three. Attempts were made to section three different pinna rachises, but in all the preservation was so poor that they revealed nothing except the gross features of anatomy (Pl. 9, fig. 3). There appears to be little or no lateral coalescence among the meristeles.

The secondary pinna and pinnules. — The rachis of the secondary pinna undoubtedly contains several meristeles, but their arrangement is far from clear in any of the sections I have prepared. Nearly a dozen specimens have been cut, but only in one were the tissues not compressed into an almost structureless coaly substance. Most were like the one shown on plate 9, figure 4. The one exception (Pl. 9, fig. 5) showed the ground tissue reasonably well, but the vascular tissues were scarcely recognizable. Present in the ground parenchyma were some arcs of large well preserved cells associated on their concave side with patches of small or crushed cells. These patches were taken to represent meristeles, the large cells, which abut directly on the convex side on to the ground tissue, representing either the endodermis or pericycle. It is likely that they correspond to the large-celled, palisade-like pericycle reported in *Paradoxopteris stromeri* by Edwards (1933). An interpretation of one section showing the possible distribution of meristeles is shown in text-figure 1 D. No secretory canals could be clearly distinguished, but some disturbances in the ground parenchyma in the peripheral region could represent them.

Little has been elucidated about the anatomy of the pinnules, except for the epidermis. Fragments of pinnules macerated slowly in alkali followed by peroxide + soda eventually produce skeletons representing the reticulate vein system. From these I conclude that there was a relatively massive fibrous tissue associated with the veins.

From cuticle preparations, the cells of the upper epidermis are seen to be quadrangular in shape, but with some tendency to be elongated over the midrib and main veins (text-fig. 1 E, left). The anticlinal walls are thick, almost straight or smoothly undulating, but never extremely sinuous (Pl. 7, fig. 4).

The lower epidermis is densely stomatic. The crowded stomata are about 50 μ long and 30-40 μ wide. They are confined to the intervein areas, but within these areas are seldom separated by more than two ordinary epidermal cells, frequently by only one (text-fig. 1 F). These non-stomatal cells have slightly undulating walls. The intervein areas are separated by 2-3 rows of more elongated cells with almost straight walls (Pl. 7, fig. 2, centre; text-fig. 1 F, left of centre). The midrib is marked by several rows of narrow elongated cells and so too apparently is the rolled over lamina margin.

Papillae such as were described by Reymanówna (1965) have not been seen, perhaps because the ordinary epidermal cells in the vein meshes are usually rather distorted. Occasionally small round cells are visible which may represent papillae (e.g., Pl. 7, fig. 3, middle right).

3. THE FERTILE FROND.

a) MORPHOLOGY.

Although it is not known definitely that the fertile frond was separate from the vegetative, such evidence as there is seems to suggest that it was. Material of *Weichselia* from other regions, most notably that from Quedlinburg in Germany (Daber, 1953; 1968) provides some positive evidence that there were separate fertile fronds : the Belgian material in no way refutes this. No primary rachis shows any evidence of a mixed fertile-vegetative condition.

Fertile parts are represented by rachises such as those shown on plate 5, figures 11-22. The cone-like soral clusters which have already been described in an earlier publication (Alvin, 1968) are borne on slender ultimate rachises, 0.5-1.0 mm in diameter, which in turn are borne in a pinnate fashion on stouter rachises. The ultimate rachises are not inserted at right angles to the penultimate, but are directed forwards in a rather striking manner and have decurrent bases (Pl. 5, fig. 16-20). The penultimate rachises are usually adaxially curved and seem to have achieved no great length; some specimens show a quite rapid attenuation towards the distal end (Pl. 5, fig. 14, 16 and 18). They are somewhat flattened laterally (about twice as deep in the adaxial-abaxial plane as wide; see section shown on Pl. 9, fig. 6) and the ultimate rachises are borne very near the adaxial edge.

Similarly, the penultimate rachises are borne along the adaxial side of stouter (primary pinna) rachises. Unfortunately, there are very few good specimens of these presumed primary rachises. The best one is probably that shown in figure 3, plate 2. This shows the adaxial side and the stumps of one row of penultimate (secondary) rachises on the left; most of those on the right are broken off at their base. Most of the primary rachis specimens are extremely fragmentary (e.g., Pl. 5, fig. 11-14) and bear only two or three bases of secondary divisions. As far as I can tell, the primary fertile rachises are of the same order of size as typical primary vegetative rachises, and their secondary rachises, although considerably stouter, are set at about the same distance apart (4-6 mm); it is thus reasonable to suppose that they were morphologically equivalent and borne in similar pedate fashion at the end of the petiole. In this connection it is worth noting the slightly divergent alignment of associated primary fertile rachises figured by Daber (1968 : text-fig. 5 C, D and E), strongly suggesting that they were borne in radiating groups as from a pedate head.

The fertile frond is therefore envisaged as consisting of a stout petiole terminating in a radiating group of perhaps quite long primary divisions. These would bear, along their adaxial side, curved secondary (penultimate) divisions. The tips of members of these two rows would thus tend to come together in pincer-like fashion over the adaxial side of the primary rachis, enclosing a narrow space. Within this space (i.e., the space separating the concave adaxial sides of the two rows of secondary divisions), the crowded ultimate divisions would lie, each carrying two rows of more or less contiguous soral clusters.

b) ANATOMY.

The specimen shown in figure 17, plate 5 was sectioned successfully and the illustrations in text-figure 2, and plate 9, figures 6 and 7 represent this specimen.

In transverse section the secondary rachis almost invariably shows three lobes on the adaxial side, the two lateral ones of which represent the decurrent bases of ultimate divisions, and the middle, the ridge running along the adaxial side of the rachis. The abaxial portion, often more or less constricted from the three-lobed adaxial part, has an irregularly ridged surface.

The secondary rachis contains quite numerous meristeles, the arrangement of which is rather irregular, at least in the middle, constricted region. There is a more or less regular arc of strands on the abaxial side, normally three prominent ones in the three adaxial lobes, and some small, often indistinct ones in the central region. It is apparently a dicyclic system.

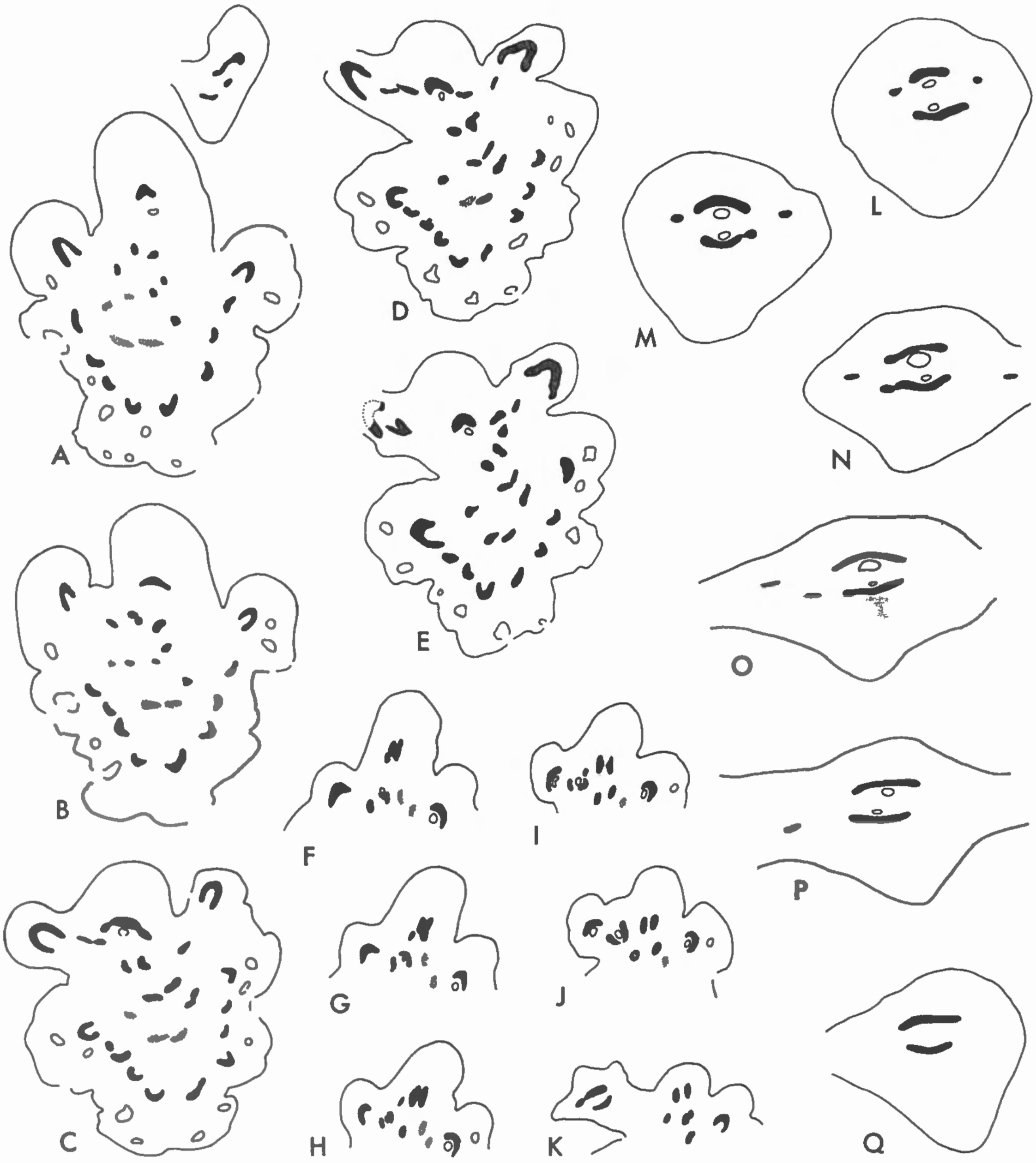

FIG. 2. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE.

A-E and F-K : two series of transverse sections through a secondary fertile rachis showing the more or less dicyclic arrangement of meristeles and their ramification in relation to emission of traces to ultimate rachises. A, section N6/10/1; B, 12/6; C, 18/2; D, 19/2; E, 19/4; F, section N7/3/2; G, 4/2; H, 5/2; I, 5/6; J, 6/3; K, 8/5. All ×15. L-Q : series of transverse sections through an ultimate rachis showing the two characteristic arc-shaped meristeles and the emission of traces to the soral clusters. L, section N7/9/7; M, 9/4; N, 8/6; O, 8/1; P, 7/3; Q, 6/2. All ×40.

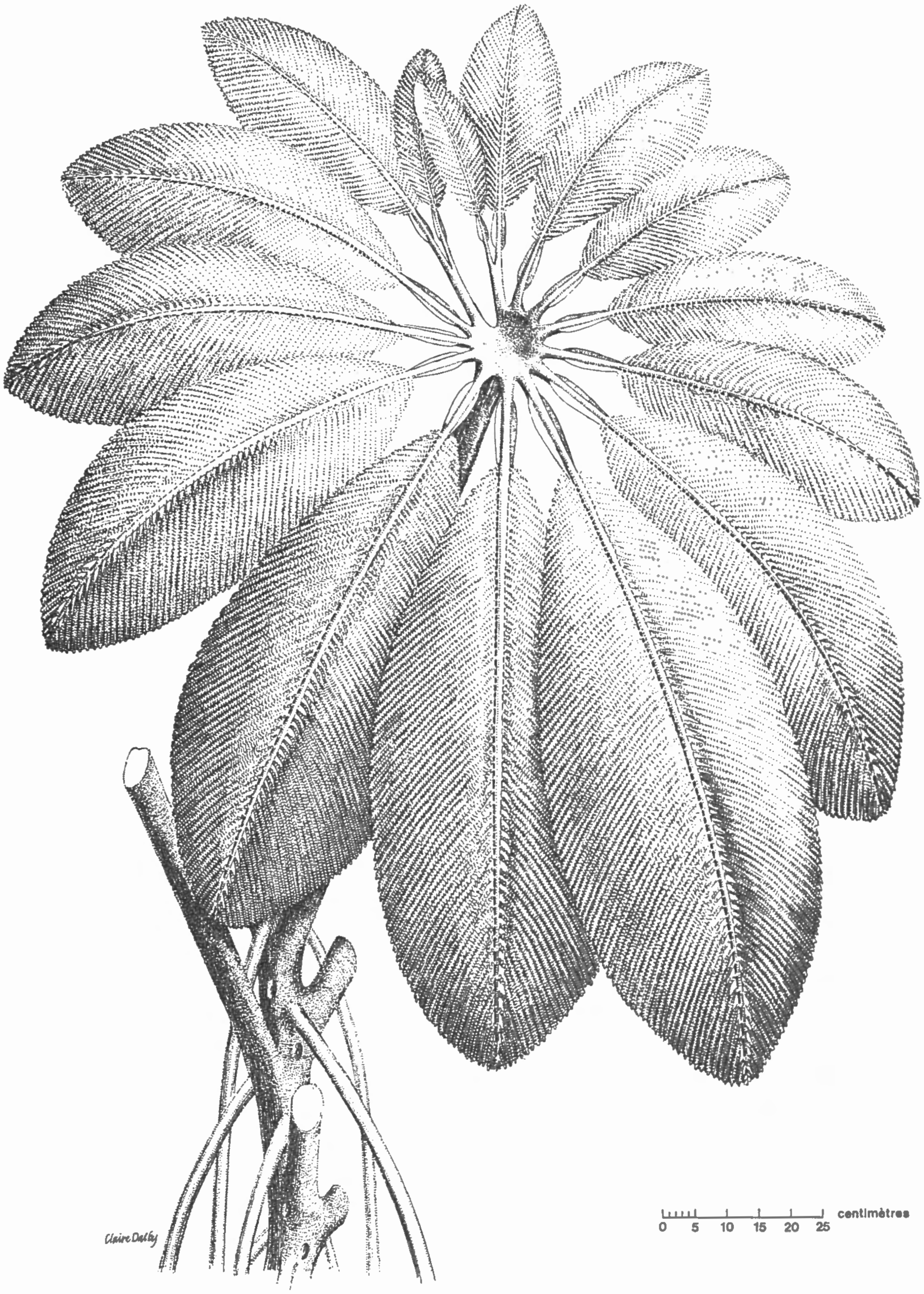

FIG. 3. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE.
Reconstruction of the plant showing the stem with petioles, rooting organs, aerophores, and one complete vegetative frond. About $\frac{1}{10}$ natural size.

The vascular supply to the ultimate rachis (text-fig. 2) consists of two meristeles of which the outer one is derived from the abaxial arc of meristeles in the secondary rachis, and the inner one partly from the central adaxial strand, and partly from the inner ring of strands. This origin can be traced in the two series of sections drawn in text-figure 2 A-E and F-K. The outer strand supplying the ultimate rachis is established at an early stage, i.e., some considerable way back in the decurrent base (text-fig. 2 A, left and right), but the inner strand is only formed at a relatively late stage, just before the ultimate rachis becomes detached (text-fig. 2 D and E, left; text-fig. 2 J and K, left). The two series of drawings in text-figure 2 (A-E and F-K) represent two different portions of the same rachis. The origin of the vascular supply to the ultimate rachis is essentially similar in both; they differ merely in the partly divided nature of the central adaxial strand in F-K.

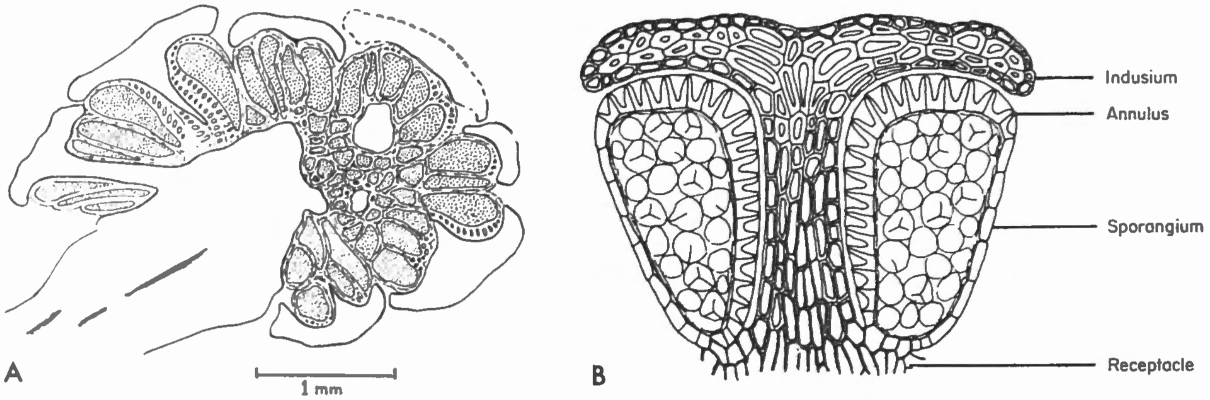

FIG. 4. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE.
A : nearly median section through a soral cluster showing the receptacle bearing crowded sori (indusia and sporangia). Section N1/9/5. B : reconstruction of a single sorus in longitudinal section. (B, reproduced with permission from *J. Linn. Soc.* [*Bot.*], 61, 1968.)

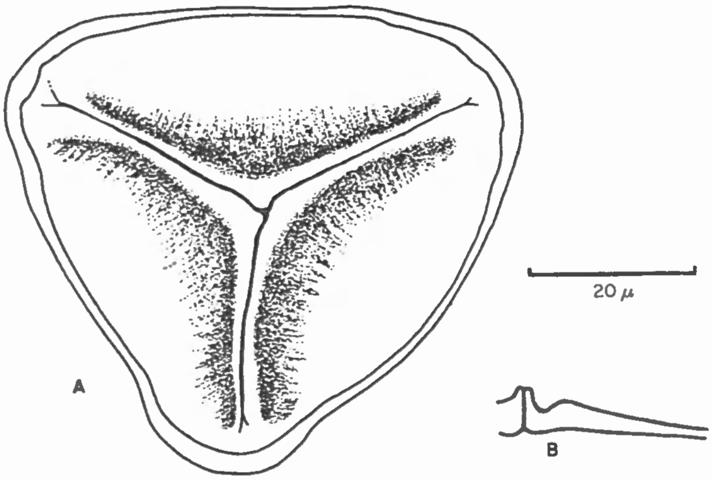

FIG. 5. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE.
A : spore in polar view. Slide NS/9. B : portion of an optical section through the exine showing the trilete ridge. Slide NS/2. (Reproduced with permission from *J. Linn. Soc.* [*Bot.*], 61, 1968.)

The ground tissue of the secondary rachis is fibrous towards the outside and parenchymatous towards the inside except for some thin and irregular strands of fibres inside each of the rings of meristeles. (These internal fibrous strands are represented by the wavy lines of lighter tissue in the lower portion of figure 6, plate 9.)

The peripheral zone of the abaxial side again contains some large secretory canals, and some of the larger meristeles also appear to have canals associated with them on their concave side, just as in the stem and rachises of the vegetative frond.

The ultimate divisions contain just two arc-shaped meristeles, both of which may sometimes show evidence of associated cavities in the ground tissue (text-fig. 2 L-Q; Pl. 9, fig. 7). Vascular supply to the soral cluster is by two very weak strands, one from each meristele (text-fig. 2 L-P).

The structure of the soral clusters and of the spores is shown in text-figures 4 and 5. They have been described in detail in an earlier publication (ALVIN, 1968), but their essential features are given here in the diagnoses in the Systematic Section.

DISCUSSION

I. — Identification of the material as Weichselia reticulata (Stokes et Webb).

The specific name was erected by Stokes and Webb (1824) for sterile frond fragments from the Wealden of England. English material, described in more detail by Seward (1894), consists usually of laminate pinnules, either isolated or attached to slender (secondary pinna) rachises, and these in turn are occasionally seen in attachment to stouter (primary pinna) rachises. Material which I have examined in the British Museum (Natural History) and the Geological Survey Museum, and also which I have collected, cannot be distinguished from the Belgian. It presents about the same degree of variation with regard to the size, shape, orientation and spacing of the laminate pinnules; indeed all the pinnae and pinnules figured here on plate 6 can virtually be matched in the English material. Cuticles which I have prepared from specimens collected in the Isle of Wight agree with those described here. I conclude therefore that the English and Belgian *Weichselia* must be placed in the same species.

The generic name, *Weichselia,* was erected by Stiehler in 1858 for remains from Quedlinburg, Germany, which he called *W. ludowicae.* This species is indistinguishable from *W. reticulata.*

II. — Comparison of the Belgian material with that from other regions.

Weichselia reticulata is remarkably widespread geographically. Outside Europe, it has been recorded from North Africa, the Middle East, Siberia, India, North America and South America. Geologically it is comparatively rare outside the Lower Cretaceous. However, Boureau and Lapparent (1951) record petrified axes of *Paradoxopteris stromeri* Hirmer from the Upper Jurassic (Kimmeridgian and Portlandian) of southern Tunisia, and Koeniguer (1966) reports records from as low as the Bathonian and up to the Cenomanian in North Africa.

Not only is the plant widespread geographically, but it is also notoriously variable in morphology. Moreover, the remains, which are usually fragmentary, tend to be preserved in rather different ways from one region to another. Although the Belgian material has now provided a more complete picture of the plant than has been obtained hitherto, its interpretation does not accord fully with previous interpretations based on material from other regions. It is therefore desirable to compare critically the Belgian material with that from some of the other more important localities.

1. Germany.

Remains of *Weichselia* are of frequent occurrence in Lower Cretaceous deposits in many parts of Europe. Of particular interest is the material from Quedlinburg and Hildesheim in Germany.

At Quedlinburg (Richter, 1906, 1909; Gothan, 1923; Magdefrau, 1932; Daber, 1953, 1968) the fossil plant remains are preserved in a sandy matrix, and although they are usually too poorly preserved to show detailed structure, the large size of many of the specimens and their presumed autochthonous origin should render them of special value for providing information about the general habit and morphology of the original plants. Hence, as **Daber** (1968) has recently published a reconstruction of *Weichselia* which differs radically from that given here, some critical comparison must be attempted.

In his first paper, **Daber** (1953) describes the fronds as consisting of two bipinnately compound portions arising from a petiole which forked near the base, and a similar organization had earlier been suggested by **Lipps** (1923) working with material from Hildesheim. These double units (« Gabelwedeln ») **Daber** depicts in his reconstruction (1968 : text-fig. 8) as arranged in a circle on the stem, and it is inferred that this single whorl or crown of vegetative fronds was borne at ground level on a short, stocky stem, in much the same manner perhaps as in those cycads which have a very short stem. The fertile fronds are envisaged as erect, but again double units borne in a single whorl above the vegetative. The idea that the leaves were borne in a single whorl on a short stem appears to rest mainly on the acceptance of specimens such as those shown in **Daber**'s text-figure 6 and plate 1, figure 2 (1968) as pieces of stem with radiating petioles preserved in situ just above a dark humic layer regarded as the soil bed upon which the plants originally grew.

It would seem to me reasonable to re-interpret such specimens as the pedate heads of large petioles and the radiating axes as the bases of the rachises of primary pinnae. **Daber**'s specimen shown in text-figure 6 (1968) would thus represent a very large pedate head some 20 cm in diameter bearing at least thirteen primary pinnae. The sulcus at the top right between two forking rachises probably represents the adaxial side. Similarly, the large specimen shown in his figure 2, plate I (1968), I would interpret as a partially exposed pedate head. In such specimens, the petiole itself, assuming it to be still present, would be orientated horizontally, i.e., parallel to the reed-bed; excavation in this direction might well yield valuable evidence supporting this re-interpretation.

Another specimen from Quedlinburg, described by **Gothan** (1923 : fig. 3) and regarded by him as a whole plant preserved in situ, is almost certainly one whole pedate frond with 11-12 primary pinnae and possibly part of the petiole exposed on the left. This specimen is of interest in relation to **Daber**'s and **Lipps**' assertion that the « fronds » (=primary pinnae) were characteristically forked at the base, for the only instance of a possible fork in **Gothan**'s specimen is on the right-hand side at the base of one of the pinnae lying immediately adjacent to what I would regard as the adaxial sulcus; the others show no evidence of forking.

Daber's account of the organisation of the fertile frond is substantially in agreement with mine as far as the ultimate and penultimate divisions are concerned, and **Lipps**' (1932) earlier observations on the fertile parts, including the spores, are also in agreement with my own on the Belgian material. However, I would interpret **Daber**'s forked fronds (1968 : text-fig. 5, D) as pairs of primary rachises of which there would have been several arising in the same pedate fashion from a petiole as in the sterile fronds. I can see no reason whatsoever for supposing that fertile and sterile members were associated in the manner suggested in **Daber**'s reconstruction.

If this re-interpretation of the Quedlinburg specimens is correct, the question remains as to whether this German material may differ in any significant way from the Belgian. In form, dimensions and arrangement of the pinnules and the secondary pinnae, the Quedlinburg material is in no way distinct; it shows a comparable range of variation. However, the paired arrangement of the bi-pinnate frond units (which I interpret as primary pinnae) remains to be explained. The Belgian material provides no definite evidence that the primary divisions arising from the pedate petiole head were paired. This is perhaps because the material is fragmentary, and the primary rachises are almost always broken off either at or only just beyond their attachment to the head. It is therefore conceivable that at some distance beyond their attachment, at least some of them may have forked. However, I have seen no bifurcating primary rachises. If one considers for a moment the frond of *Matonia pectinata,* here the pedate organisation is usually interpreted as basically a dichotomous system in which at all points of branching except the first and last, the dichotomies are unequal in such a way that one shank produces a primary pinnate segment whilst the other contributes to the recurving arms which were established by the first (equal) dichotomy. The last dichotomy on each side results effectively in two (often very unequal) pinnate segments. It is therefore possible that in *Weichselia* the members on either side of the adaxial sulcus dichotomised once (or perhaps more) to give two or more bi-pinnate segments. This idea is supported by DABER's specimen (1968 : text-fig. 6) and GOTHAN's (1923 : fig. 3).

An alternative explanation of the paired arrangement of detached primary pinnae might be that they tended to adhere together in small groups or pairs after the break-up of the pedate head due to differences in the degree of fusion between one segment and its neighbours in the *Matonia*-like system; for, as has already been suggested in the description, the « *Matonia* » interpretation implies some degree of fusion amongst the basic members in order to give the massive discoid « head » of *Weichselia.*

Reference has already been made in the description (p. 10) to the aphlebiae-like wings at the bases of the main frond segments (primary pinnae) reported by both DABER (1968) and LIPPS (1923). I have not been able to demonstrate this feature in the Belgian material, but probably only because of the more fragmentary nature of the specimens and the rarity of basal parts of pinnae. Accordingly, I have ventured to show such wings in the reconstruction (text-fig. 3).

Another problem is the apparent absence of petioles and stems from the German localities. If the Quedlinburg specimens are really autochthonous, as believed by DABER and others (*loc. cit.*), and the comparatively unbroken nature of many of the frond specimens gives some support to the geological evidence for this theory, one might expect to find stems and petioles in close association with the other frond remains. I believe the larger organs may be represented by *Stiehleria similidae.*

STIEHLER (1857) described some axes under the name *Pandanus similidae* which he interpreted as monocotyledenous. In 1953, DABER, evidently following a similar line of thought, interpreted these axes, which he placed in a new genus, *Stiehleria,* as false stems consisting of sheathing leaves. The appearance of some of the specimens certainly invites such an interpretation, for example, the specimen shown in DABER's plate 7, figure 2, in which different striated layers are exposed, the inner ones being more finely striated than the outer. An alternative explanation of such specimens would be to regard them as solid axes decorticated to different levels, the striations representing exposed vascular strands. The cross-section shown in another of DABER's figures could also be interpreted as belonging to a solid axis containing a number of concentric rings of strands, rather than as a false stem with « leaf-layers ». The preservation of all the *Stiehleria* specimens is extremely poor, and none shows the rugosity characteristic of the *Weichselia* major axes. Indeed, it is difficult to tell whether any of the illustrated specimens are not to some degree decorticated. They show no clear leaf-bases and no convincingly attached roots, although roots were mentioned and figured by DABER. The « astnarben »-like structures are remarkably similar in appearance to the marks on such specimens as that shown here on plate 3, figure 3, which are believed to represent aerophores in the decorticated condition.

Although the evidence for the identity of *Stiehleria similidae* and *Weichselia reticulata* cannot for the present be regarded as conclusive, I believe that there is a strong probability that this will be proved by careful re-examination of the Quedlinburg fossils.

2. **Holma Sandstone** (found in Germany).

The partially petrified portion of a *Weichselia* frond described by SCHUSTER (1930) from a Holma Sandstone boulder is of importance as the only example of material with internal structure preserved hitherto reported from Europe. Although the specimen was fragmentary, its preservation was in some respects superior to that of the Belgian material. It displayed histological features, such as the structure of the epithelium of the secretory ducts, which I have not been able to observe in the Belgian lignite. The general pattern of the anatomy, both of the primary and of the secondary rachis, is, as far as I can see, the same, except only that in SCHUSTER's specimen there is no evidence of the breakdown of tissues (interpreted here as a possible secretory duct) on the concave side of the C-shaped meristeles and longitudinal rows of crystal-containing cells were present in the ground tissue. KOENIGUER (1966), who places this material in *Paradoxopteris stromeri*, regards it as a distinct variety largely on the strength of this last character. I have not recognized any crystal-cells in the Belgian material.

From another Holma Sandstone boulder, NATHORST (1891) described fragments of *Weichselia pinnae* which he named *W. erratica* because of the unusually large size of some of the pinnules. As EDWARDS (1933) pointed out, this species cannot be maintained on the strength of such a character. Associated with the vegetative fragments NATHORST also described a portion of a fertile fern frond which he compared with the recent genus *Onoclea* : it is an entirely typical piece of fertile *Weichselia* with globular soral clusters.

3. **England.**

The English material, like most *Weichselia* material from elsewhere, is very fragmentary. Most of it is preserved as small charred fragments lying in a sandy matrix together usually with a small proportion of uncharred fragments. Only very rarely are the secondary pinnae found in attachment to the primary rachises. No fertile specimens have been reported, a rather surprising fact in view of the frequent abundance of vegetative fragments (*).

Examination of a sample of typical material collected from Shepheard's Chine, Isle of Wight, has revealed that, apart from the abundant pinnules and pieces of secondary pinnae, there were also frequently present small pieces of primary rachis with the bases of secondary pinnae still attached, and also larger pieces of charcoal in which broken surfaces usually showed coarse longitudinal striations consistent with their interpretation as meristeles : I believe therefore that these associated fragments may represent pieces of the larger organs of the plant. Maceration of a small piece of the matrix in hydrofluoric acid yielded several small peltate structures agreeing completely in size and form with typical indusia of *Weichselia*.

This kind of material then, probably represents a general *Weichselia* débris deposited in a sandy sediment perhaps after a fire in the *Weichselia*-dominated vegetation of a nearby land surface. The material described recently from Poland by REYMANÓWNA (1965) is evidently very similar.

(*) A fragment of fertile material with two soral clusters has now been recovered by bulk macerating a sample of *Weichselia*-containing matrix collected in the Isle of Wight.

4. North Africa.

Material from North Africa consists of fragments of vegetative pinnae and petrified axes (*Paradoxopteris*). The leaf fragments appear to differ in no significant way from European material.

Paradoxopteris stromeri (HIRMER) HIRMER, discovered originally at the Baharia Oasis in the Libyan Desert, Egypt, and reported since from several other localities in North Africa (See EDWARDS, 1933; BOUREAU and LAPPARENT, 1951; KOENIGUER, 1966), was interpreted by EDWARDS (1933) as representing rachises of *Weichselia*. EDWARDS, however, did not accept BOMMER's theory of the pedate construction of the frond. If he had had access to the evidence upon which BOMMER's theory was founded, he would probably have regarded the *Paradoxopteris* specimens as petioles. The comparison summarised in Table I suggests that they are more comparable with the petiole than with either stem or the (pinna) rachis.

The question as to whether *Paradoxopteris stromeri* represents the same natural species as *Weichselia reticulata* from Belgium cannot yet be settled unequivocally, for, bearing in mind the difference in the mode of preservation, I am uncertain of the significance of the structural differences which they show. The notable differences are the following :

1. The rather regular occurrence and distribution of accessory strands in *Paradoxopteris*. In no specimen of *Weichselia* that I have examined have the accessory strands been as regular in their occurrence as they evidently are in HIRMER's original material of *Paradoxopteris*. (They seem to be somewhat less regular in some of the material examined by EDWARDS and KOENIGUER.) In the Belgian *Weichselia* they are undoubtedly sometimes present, most notably in the petiole; there are few or none in the stem, at least in the outer part. However, because of poor preservation it is often difficult to distinguish small accessory strands from secretory ducts; it is also possible that they may sometimes have become completely obliterated in the crushed ground tissue.

2. Secretory ducts. Frequently in the Belgian *Weichselia* there is a disturbance or breakdown of the tissues in the ground tissue on the concave side of the C-shaped meristeles. I have suggested that these may represent secretory canals (see p. 8). There is no indication that canals occur in this position in *Paradoxopteris*, though examination of EDWARDS' slides in the British Museum (Natural History) has revealed that frequently, one, or more often two, small break-down cavities do occur in this position. Two meristeles shown by EDWARDS (1933 : Pl. 14, fig. 3 and 4) each have two such cavities, in spite of the fact that in one of them (fig. 4) the other tissues appear almost perfectly preserved. It is therefore possible that these cavities are comparable in both *Paradoxopteris* and the Belgian *Weichselia*, and that they represent not canals but merely disruption of the tissues that occurred at a point of weakness in the ground tissue related to the « C » shape of the main meristeles. Whether they developed during growth or only after death of the tissues cannot be determined. KOENIGUER (1966) reports much variation in the frequency of secretory ducts in *Paradoxopteris*.

3. Palisade-like pericycle in *Paradoxopteris*. This feature was stressed by EDWARDS as a regular feature of the petrified axes. I have seen no clear evidence of it in any of the sections of the Belgian *Weichselia*, though the arcs of large cells described in the secondary vegetative rachis (see p. 13) may represent the same structure. My examination of EDWARDS' slides revealed that only in a very small minority of meristeles was the preservation good enough to make it possible to discern this layer; it may not therefore have been as regular a feature as EDWARDS assumed. At the same time, the preservation of the Belgian material makes it impossible to be sure that such a pericycle was not present.

TABLE I. — **Comparison of the main features of** Weichselia **and** Paradoxopteris stromeri.

	Stem of *Weichselia*	Petiole of *Weichselia*	Primary Pinna Rachis of *Weichselia*	*Paradoxopteris stromeri*
No. of main meristele rings	< ca 20	< ca 12	< ca 5	< 11
Accessory strands	Few or none	Present	Present	Present
Lateral coalesence among main meristeles	None in outer rings, but some possibly towards centre	Coalesence on abaxial side in smaller specimens but not larger	Little or none	None

4. Spacing of the meristele rings. In none of the *Paradoxopteris* specimens do the inner meristele rings become so markedly closer together as they appear to consistently in all the larger axes of the Belgian material. This could conceivably be due, however, to the compression and shrinkage of the lignite which has been greater towards the centre where the ground tissue contains relatively less thick walled tissue than in the peripheral region.

Apart from these characters, there is nothing to separate the two taxa. It is possible that we are dealing with a highly polymorphic species or a group of closely related species, and in this connection it is of interest that KOENIGUER, who regards the two taxa as representing the same plants, nevertheless recognises three structurally distinct varieties in *Paradoxopteris stromeri*.

5. South America.

The specimens of *Weichselia* from Peru have attracted interest not only because of their geographical remoteness from the Eurasian-North African area, but also because of the early report of supposed fertile parts (NEUMANN, 1907; ZEILLER, 1914) and the occurrence of large axes in association with the vegetative pinnae, which led ZEILLER to believe that the frond was tripinnate. I can add little to the comments of EDWARDS (1933) except to say that these large axes are, I believe, pieces of petiole. The scars that they show, which ZEILLER (1914 : Pl. 21, fig. 12, 13) regarded as the places where primary pinnae were attached, are remarkably similar in appearance to the scars seen in such a specimen as that shown here on plate 3, figure 3, which I interpret as possible aerophores. None of the Peruvian axes show surface tubercles, but this is not surprising if they were all decorticated.

The reflexed basal pinnules, which BERRY thought distinguished the Peruvian leaves as a separate species, have been shown to occur, and indeed were probably a regular feature, in European and other material.

I agree with both BERRY (1928) and EDWARDS (1933) that the supposed fertile specimens described by ZEILLER (1914) cannot be accepted either as being unequivocally fertile or indeed as belonging to the same kind of plant as the vegetative material, for they do not show clearly the characteristic net venation. The specimen reported by STEINMANN (1929) on the other hand, and described under a new name, *Peruviophyllum minutifolium*, is very probably a fragment of a fertile frond. The small appendages on the slenders laterals are probably soral clusters.

6. Other regions.

Fragments of vegetative pinnae have been reported from many localities over a wide geographical area (see below). The mostly fall well within the range of variation found in the Belgian material. However, two records are perhaps worthy of note. Some of the fragments reported by **Edwards** (1926, 1933) from the Middle East have unusually large pinnules up to 17 mm long, but they are not consistently larger than in European material. Another noteworthy specimen is that described by **Berry** (1928) from Texas in which the main (pinna) rachis bore laminate pinnules between the insertion of the secondary pinnae. However, this character has also been reported in a specimen from Belgium described by **Seward** (1900), which obviously represented an extreme apex of a primary pinna. **Berry**'s specimen was probably also from near the apex, so perhaps this was a regular feature of the distal end of the primary pinna.

III. — Geographical Distribution.

Vakhrameev (1964, p. 209, fig. 33) has recently summarised the distribution of *Weichselia reticulata* in the Lower Cretaceous of Eurasia. It extends from England and Portugal through western, central and eastern Europe to central Siberia and the Far East (Primorsk Kray). Further to the south it has been recorded in several localities in North Africa (**Boureau** and **Lapparent**, 1951; **Koeniguer**, 1966), the Middle East (**Edwards**, 1929, 1933), Kazakhstan and Uzbekistan (**Vakhrameev**, 1964) and north-central India (**Bose** and **Sukh Dev**, 1959). Further south still, its occurrence can now be recorded from Kailta in the Wergudud area of northern Kenya. This record, not previously published, is based on some quite typical specimens, consisting of primary and secondary pinnae with pinnules, in the collection of the Palaeontology Department, British Museum (Natural History) (Specimen no. V 32250).

In the Americas, the specimens from Peru must, at least tentatively, be accepted as *Weichselia reticulata*. **Schlagintweit** (1919) reported it from Venezuela but did not illustrate specimens. In North America, fragments have been recorded from Dakota (**Fontaine**, 1899) and Texas (**Berry**, 1928).

In spite of its widespread distribution, it was probably not cosmopolitan. It has not been recorded from Australasia, Southeast Asia (its occurrence in China and Japan seems doubtful), South Africa, southern South America, northern North America and northeastern Siberia. Its zone of distribution was probably a broad tropical to warm temperate belt. Its occurrence on both side of the Atlantic is not surprising if in fact the opening of the South Atlantic was not completed until Cretaceous times (**Hurley**, 1968).

IV. — Biology.

Ecology. — *Weichselia* has generally been regarded as a zerophyte because of its zeromorphic characters and also because the sandy deposits in which it is often found have sometimes been regarded as dune-formations laid down under arid conditions. **Daber** (1968) has recently suggested that it may have been a plant of wet soils in maritime situations, but probably exposed to strong insolation. I do not think that there is yet available any conclusive evidence about its ecology. One point of possible ecological significance worth noting, however, is the comparative rarity with which *Weichselia* remains occur in intimate association with other plant remains. This may mean that it was the dominant species of the community in which it generally grew.

Habit. — *Weichselia* was undoubtedly a remarkably massive fern. The stem shows no evidence of dorsi-ventrality, so it was probably not a creeping rhizome. Most ferns having an upright stem have also very closely arranged leaves; *Weichselia* did not. The rooting organs, if this interpretation of the downwardly directed organs on the stem is correct, are unique among ferns; they are somewhat reminiscent of the stout aerial prop-roots of certain tropical monocotyledons such as *Pandanus*.

V. — **Systematic position.**

That *Weichselia* shows some affinity with the Matoniaceae is indisputable. The sori with their indusia are of a kind known only in this family. The spores are very similar and the basic pedate organisation of the frond is strictly comparable, though this also occurs in certain other ferns.

However, in spite of these similarities, there is a wide gulf between *Weichselia* and any living or known fossil member of the Matoniaceae. The most notable differences are the bipinnate nature of the primary divisions of the frond, the stem with its presumed rhizophores, the complex polycyclic dictyostele, the presence of secretory ducts, and the non-laminate fertile pinnules with their tight clusters of sori. Accordingly, I agree with ZIMMERMAN (1959) that it should be placed in a separate family. It may be envisaged as a highly specialized derivative of an early Matoniaceous stock.

SYSTEMATIC SECTION

Order **FILICALES** (*)

Family **WEICHSELIACEAE** Zimmermann, 1959.

Diagnosis. — *Leptosporangiate* ferns. *Stem* and petiole of adult plant with a complex polycyclic dictyostele. Secretory ducts present. *Frond* with primary divisions borne in a pedate manner on the petiole. Ultimate divisions of fertile frond non-laminate, bearing two rows of soral clusters. *Soral cluster* consisting of a receptacle bearing tightly packed sori. *Sorus* simple, consisting of a ring of sporangia covered by a peltate indusium. *Sporangia* large, sessile, with a slightly oblique, uniseriate annulus.

Genus WEICHSELIA Stiehler, 1857.

Weichselia reticulata (Stokes et Webb) Fontaine.

Synonymy (For early synonymy, see Seward, 1894).

1891 *Weichselia erratica* Nathorst, p. 24, pl. 1, fig. 1-4.
1891 « *Onoclea*-like fern » Nathorst, p. 24, pl. 1, fig. 5-7. (Portion of fertile frond.)
1900 *Conites minuta* Seward, p. 28, pl. 4, fig. 60-62. (Soral cluster.)
1907 *Equisetites peruanus* Newmann, p. 78, pl. 2, fig. 1, 2. (Petioles or stem fragments.)
1914 *Weichselia peruviana* (Neumann) Zeiller, p. 654, pl. 2, fig. 2-13, text-fig. D_1, D_2, E.
1921 *Smeystersia minuta* (Seward) Fraipont, p. 51, pl. 1, fig. 1, 2. (Soral cluster.)
1930 *Weichselia reticulata* var. *erratica* (Nathorst) Schuster, p. 73. (Name only.)

Paradoxopteris stromeri (probably conspecific with *Weichselia reticulata*).

1925 *Osmundites* (?) *stromeri* Hirmer, p. 5, pl. 1, fig. 3, pl. 2-5.
1927 *Paradoxopteris stromeri* (Hirmer) Hirmer, p. 609.

Some specimens probably representing *Weichselia reticulata* but recorded under different names. (List not exhaustive.) (**)

1857 *Pandanus similidae* Stiehler, p. 75, pl. 14. (? stems and petioles.)
1876 « *Equisetites* sp. » Trautschold, p. 204, pl. 18, fig. 1, 3, (*not* fig. 2). (? petioles or rachises.)
1876 « *Calamites* sp. » Trautschold, p. 203, pl. 18, fig. 10. (? petiole.)
1899 *Equisetum virginicum* Fontaine : Fontaine *in* Ward, p. 650, pl. 160, fig. 1. (? petioles.)
1929 *Peruviophyllum minutifolium* Steinmann, p. 105, fig. 113. (? portion of fertile frond.)
1953 *Stiehleria similidae* (Stiehler) Daber, p. 410, pl. 5-10.

(*) If the classification given by Pichi-Sermolli (*Uppsala Univ. Arsskr.*, 6 : 70-90, 1958) is accepted, the Weichseliaceae would fall within the order Matoniales.

(**) Since this paper was submitted for publication Remy and Remy (*Argumenta Palaeobotanica*, 3 : 91-129, 1969) have published an account of a petrified axis with a polycyclic system of steles from the Middle Barremian of Alstätte, West Germany, wich they named *Alstaettia andersoni* Remy et Remy, and which I believe may represent the interior part of a large *Weichselia* stem.

Type Specimen. — Stokes and Webb (1824) gave two illustrations of material from Tilgate Forest, near Cuckfield, Sussex : (1) a small block on which were preserved three fragments of vegetative pinnae (Pl. 46, fig. 5); (2) a drawing of some pinnules showing the venation (Pl. 47, fig. 3). I have been unable to trace this material, and it must be presumed lost. I therefore propose to select a *neotype*, namely, that illustrated by Seward (1894) as plate 10, figure 3 and text-figure 12 (and also in Seward's « Fossil Plants », vol. II, fig. 333 A, p. 495). This specimen, which is one of the most complete from the English Wealden, is also from Sussex, but is not precisely localised. It is specimen V 2630 in the collection of the British Museum (Natural History).

Emended Diagnosis. — *Stem* massive, erect or sub-erect, bearing petioles arranged in a loose spiral, and downwardly directed (? rooting) organs associated with the petiole bases; surface rough, and with scattered elliptical « scars » (? aerophores). Stem with numerous (up to about 20) concentric rings of meristeles.

Petiole straight, up to 5 cm or more in diameter, typically with a rough surface, terminating in a flattened head from which radiate up to about 15 primary divisions of the frond (primary pinnae); petiole with up to about 12 rings of meristeles.

Primary pinnae up to 1 m or more in length, broadly lanceolate, bipinnately compound; rachis up to 2 cm wide at base; abaxial side of rachis more or less striated throughout length, sometimes also rough at base in large specimens; adaxial side smooth or only finely striated; rachis winged and without secondary pinnae near base; with up to about 6 rings of meristeles.

Secondary pinnae of vegetative frond 6-15 mm apart (typically about 8 mm), up to 25 cm or more in length, bearing two rows of pinnules inserted near the adaxial side of the rachis; first pinnule borne on basiscopic side; rachis 0.5-1.2 mm broad, 0.6-2.0 mm thick; with rather irregularly scattered meristeles; pinnules tending to stand erect in the more proximal parts of secondary pinnae; complanate distally.

Vegetative pinnules variable in size and shape; typically 3-5 mm long, 1.3-2.3 mm wide; oblong with rounded ends; often slightly sigmoid; attached along whole breadth of base, constricted or straight on acroscopic side, slightly constricted, straight or slightly decurrent on basiscopic side; adjacent pinnules becoming adnate and more pointed in extreme distal parts of secondary pinnae; adaxial surface of pinnule convex often with slightly depressed midrib and rolled-over margins. Midrib and veins more prominent on adaxial side. Typically 4-5 vein meshes between midrib and margin. Fibrous tissue associated with veins. Hypostomatic. Upper epidermis of isodiametic cells with smooth or slightly undulating walls; more rectangular over midrib. Lower epidermis with large crowded stomata in the intervein areas; non-stomatal epidermal cells with straight or slightly undulating walls; cells over veins more rectangular; cells over midrib and leaf margins narrow, elongated.

Secondary pinnae of fertile frond stouter than those of vegetative, curving adaxially so that the two rows enclose a space over the adaxial side of the primary pinna rachis. Two rather irregular rings of meristeles.

Ultimate fertile divisions (*pinnules*) filiform, non-laminate, borne in two rows on the secondary pinna rachis and directed adaxially and forwards into the space enclosed by the secondary pinnae, bearing two rows of globular soral clusters. Typically containing only two meristeles.

Soral cluster up to 4 mm in diameter, sessile, consisting of (12-) 22 (-44) tightly packed sori.

Sorus of about 12 sporangia covered by a thick sclerotic indusium.

Sporangia sessile ovoid, c. 0.8 mm × 0.3 mm.

Spores c. 50-80 μ in diameter (mean 67.2 μ) (*), trilete tetrahedral with convex distal face. Amb rounded triangular. Exine smooth. Arms of trilete mark extending nearly whole radius; ends often faintly unequally bifurcate. Lips simple membranous extensions of the exine 2-3 μ high. Each contact area thickened along an arc 5-10 μ wide close to the trilete arms; exine of thickened arc up to 5 μ thick, thinning rather gradually towards the interradial equatorial region to a minimum of about 1.5 μ. Exine in radial equatorial and distal regions up to 3.0 μ thick.

(*) Dimensions are variable according to the maceration technique used. Those given refer to samples macerated by the method described *in* ALVIN (1968).

APPENDED NOTE

Prof. **Ch. Bommer**, in his sole publication on the Belgian Wealden flora (1911), gave a reconstruction of *Weichselia,* similar in all essentials to the one given here, and based on his observations on the extensive suite of specimens which he had collected. Unfortunately, he did not, in this preliminary note, present the evidence upon which his conclusions were based, and in consequence a number of subsequent workers have expressed doubts about the validity of his conclusions. This memoir is presented with the hope that it will do appropriate honour to the name of the late **Ch. Bommer** and that it will bear witness not only to his skill as a collector, but also to his integrity as a scientific observer.

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CONTENTS

PLATE I

EXPLANATION OF PLATE I.

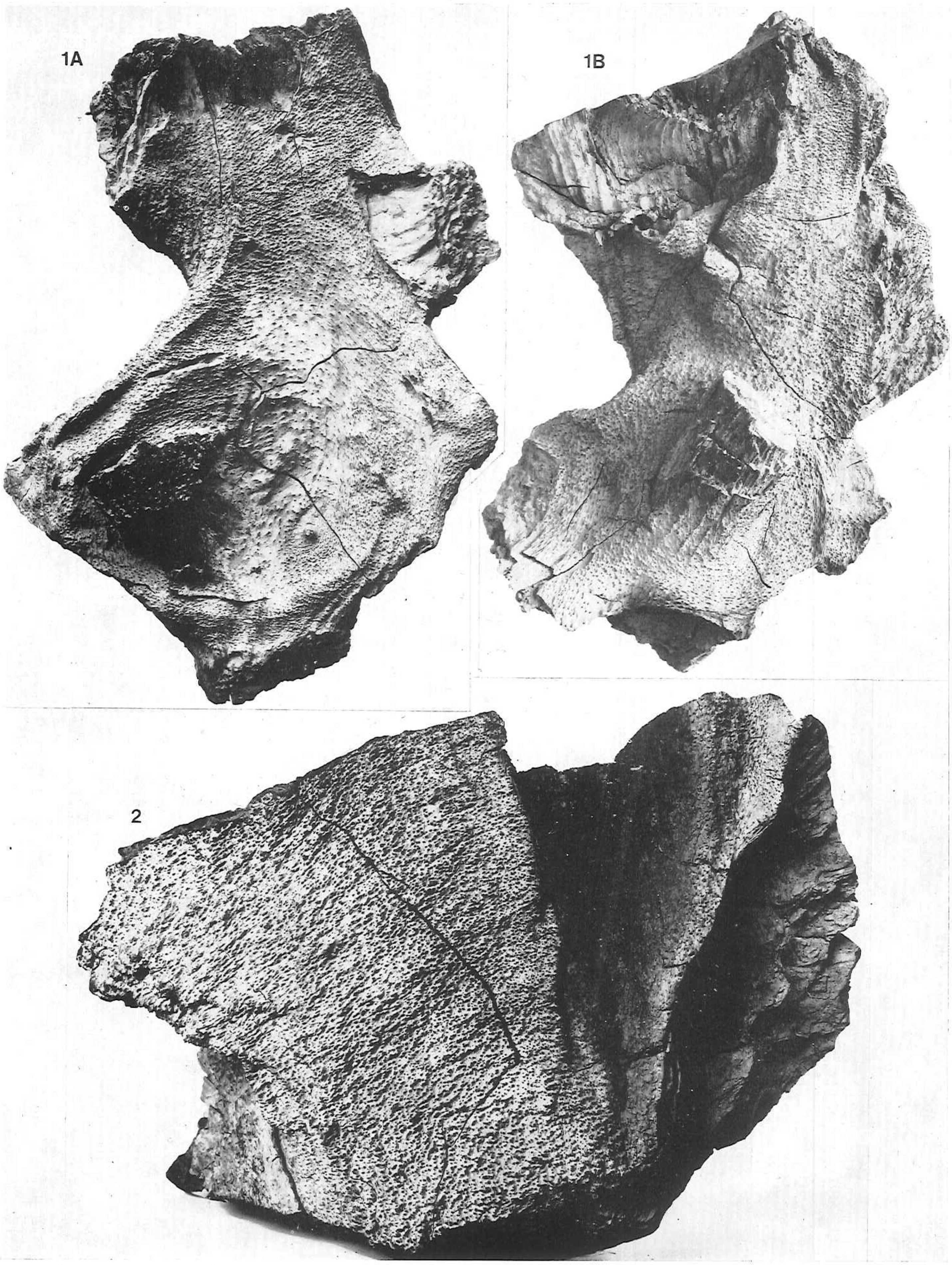
Weichselia reticulata (STOKES et WEBB) FONTAINE.

FIG. 1. — A, B, two sides of a piece of stem, showing the broad, broken-off bases of petioles and the bases of two presumed rooting organs. ×1. (Photographs by Ch. BOMMER.)

FIG. 2. — Piece of stem showing evidence of a dichotomy. ×2. (Photograph by Ch. BOMMER.)

⁂

Note. — Except where otherwise stated, all specimens shown in the Plates are from Bernissart Mine, Siege no. 1 (Négresse).



K. L. ALVIN. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE
from the Wealden of Belgium.

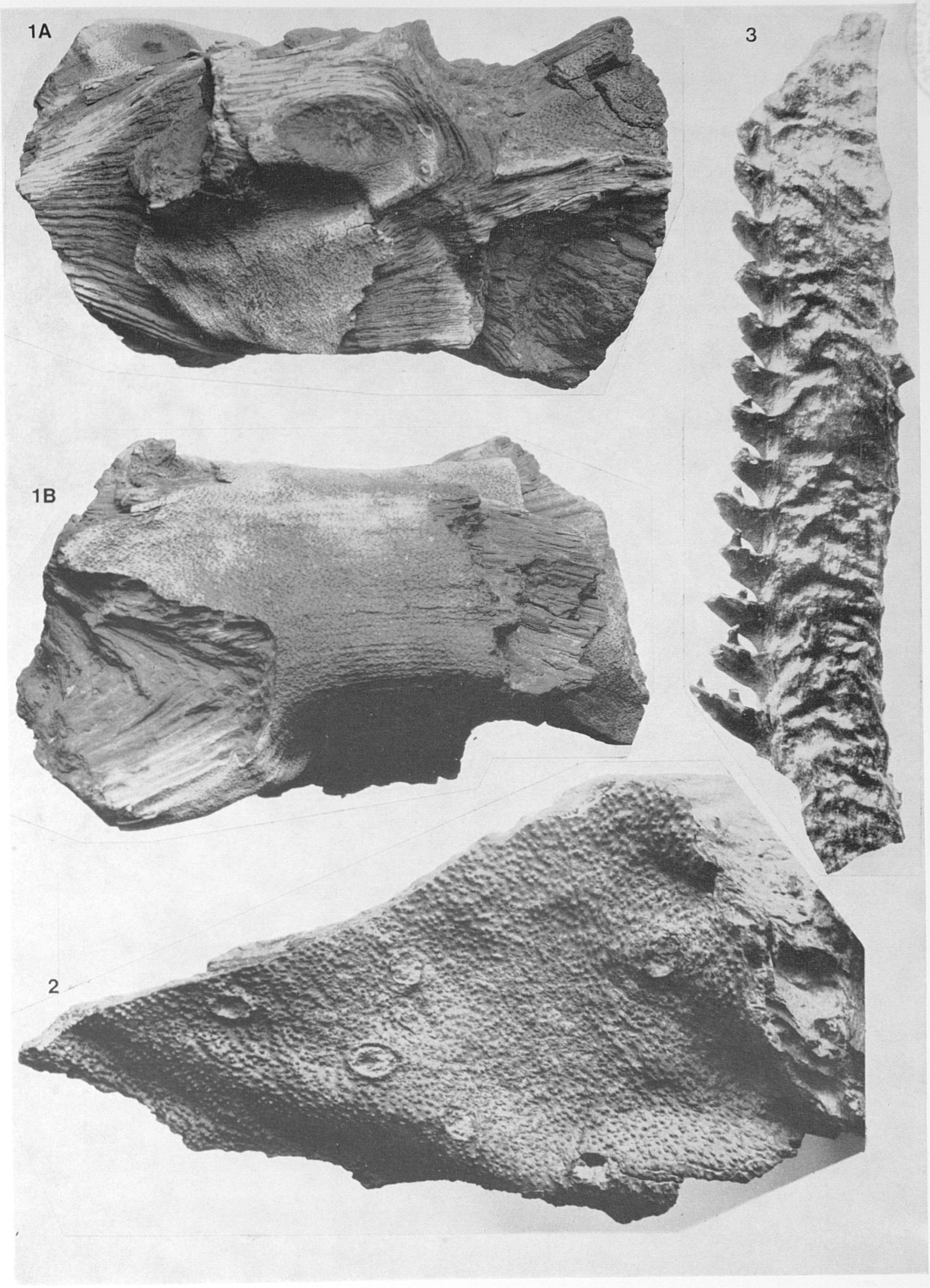
EXPLANATION OF PLATE II.

Weichselia reticulata (Stokes et Webb) Fontaine.

Fig. 1. — A, B, two sides of a piece of stem, showing broken-off petiole bases and, in 1A, presumed aerophore associated with two small, crater-like scars. ×¾. (Photographs by Ch. Bommer.) From Baudour. Specimen no. 500.

Fig. 2. — Small piece of stem or petiole, showing the surface tubercles and several small crater-like scars. ×3. (Photograph by Ch. Bommer.)

Fig. 3. — Portion of the primary pinna rachis of a fertile frond (adaxial side), showing, on the left, a row of broken-off secondary pinnae with the bases of fertile pinnules. ×3. (Photograph by Ch. Bommer.)



K. L. ALVIN. — *Weichselia reticulata* (Stokes et Webb) Fontaine
from the Wealden of Belgium.

EXPLANATION OF PLATE III.

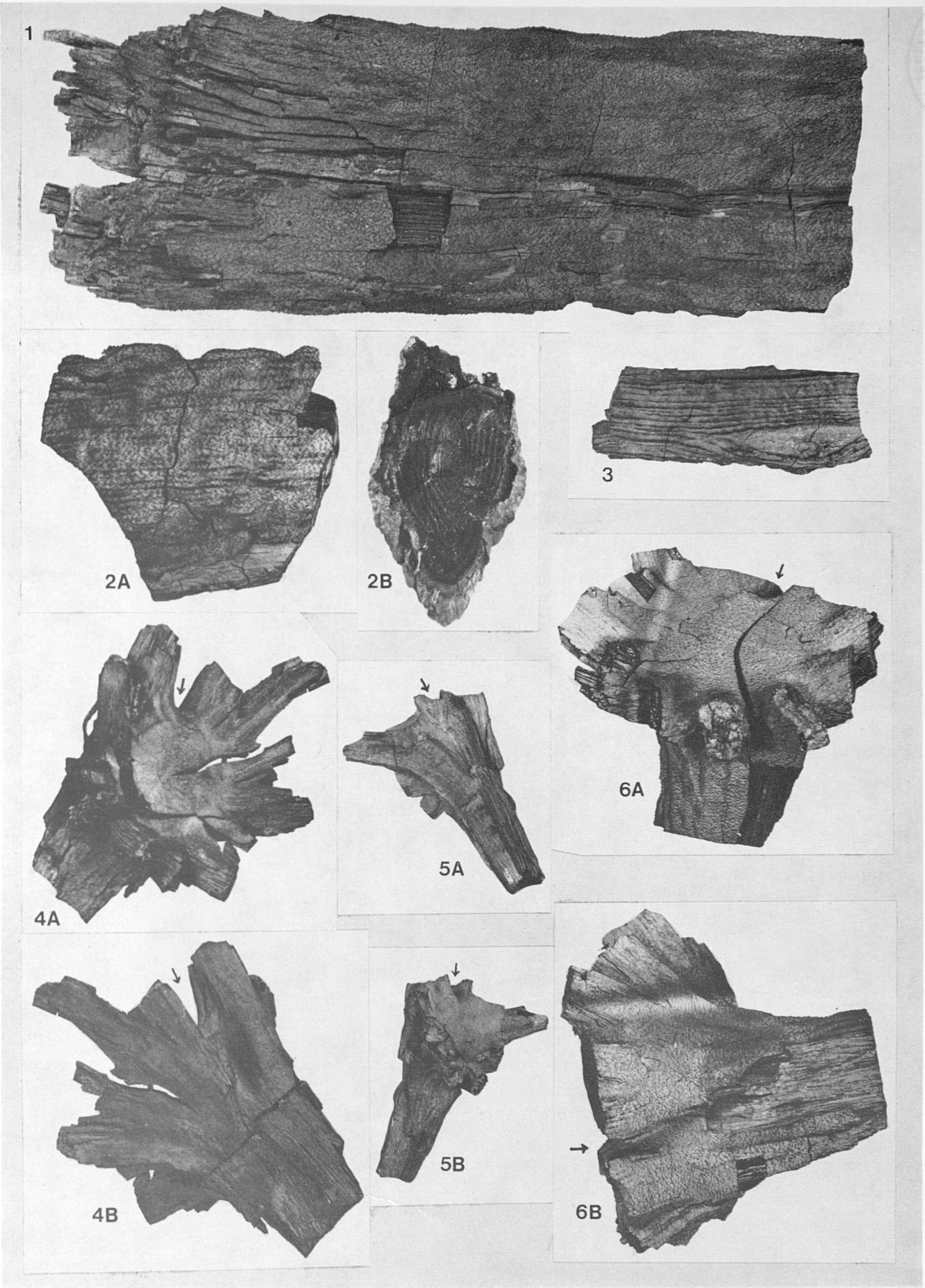
Weichselia reticulata (STOKES et WEBB) FONTAINE.

FIG. 1. — Portion of a large petiole. No. 976. × 1.

FIG. 2. — A, B, portion of a large petiole. Broken end (2B) showing the polycyclic stelar system. × 1.

FIG. 3. — Decorticated specimen (? portion of a petiole) showing a parting in the striations probably representing an aerophore. No. 1202. × 1.

FIG. 4-6. — Three petiole heads showing the pedately arranged bases of the primary rachises of the frond. The arrow in each case indicates the position of the adaxial sulcus. Fig. 4, no. 1357; Fig. 5, no. 1048; Fig. 6. From Hautrage. All × 1.



K. L. ALVIN. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE
from the Wealden of Belgium.

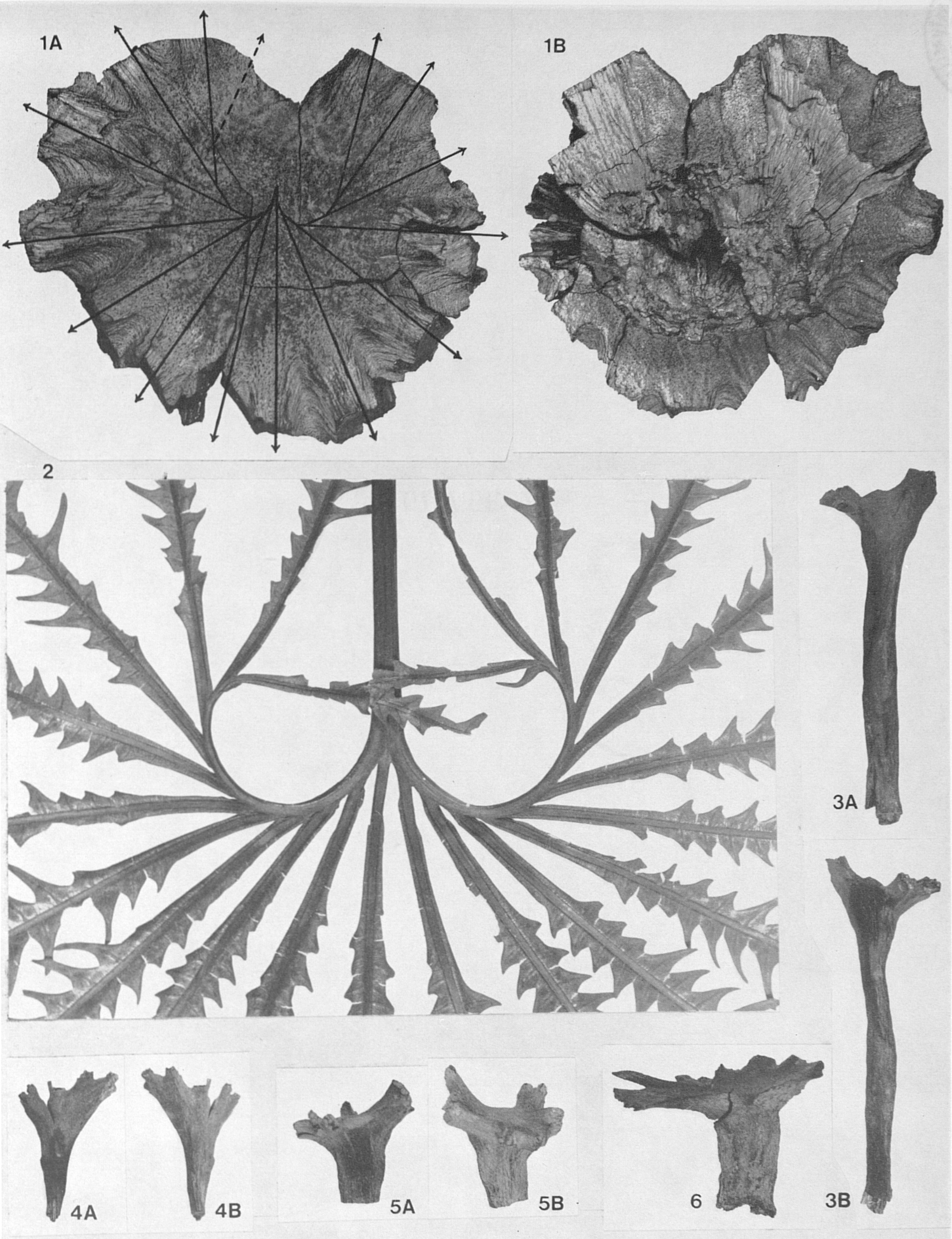
EXPLANATION OF PLATE IV.

Weichselia reticulata (STOKES et WEBB) FONTAINE.

FIG. 1. — A, B, two sides of a large pedate head; adaxial sulcus at the top. Arrows in 1A represent an interpretation of the structure in terms of a *Matonia*-like system. No. 1056 × 1.

FIG. 2. — *Matonia pectinata*. Portion of the adaxial side of a frond.

FIG. 3-6. — Four small petiole heads, showing the smoother surface and the tendency for the head not to be so markedly reflexed as in the larger specimens. Fig. 3, no. 1059; Fig. 4, no. 1050; Fig. 5, no. 1054; Fig. 6, no. 1036. All × 2.



K. L. ALVIN. — *Weichselia reticulata* (Stokes et Webb) Fontaine
from the Wealden of Belgium.

EXPLANATION OF PLATE V.

Weichselia reticulata (STOKES et WEBB) FONTAINE.

FIG. 1, 2. — Two scars on portions of stem or petiole cortex, believed to represent aerophores. Fig. 1, no. 981; Fig. 2, no. 1065. Both ×1.

FIG. 3. — A, B, two sides of a primary pinna rachis, probably representing a portion near the base. Arrows indicate small secondary pinna scars. No. 1158. ×1.

FIG. 4. — Primary pinna rachis; adaxial side. No. 1439. ×1.

FIG. 5. — Primary pinna rachis, compressed laterally. Secondary rachis marked by the arrow is shown in Text-fig. 1, A-C. No. 1400. ×1.

FIG. 6-8. — Primary pinna rachises. Fig. 6, no. 1184; Fig. 7, no. 1390; Fig. 8, no. 1106. Fig 6, 7, ×1; Fig. 8, ×2.

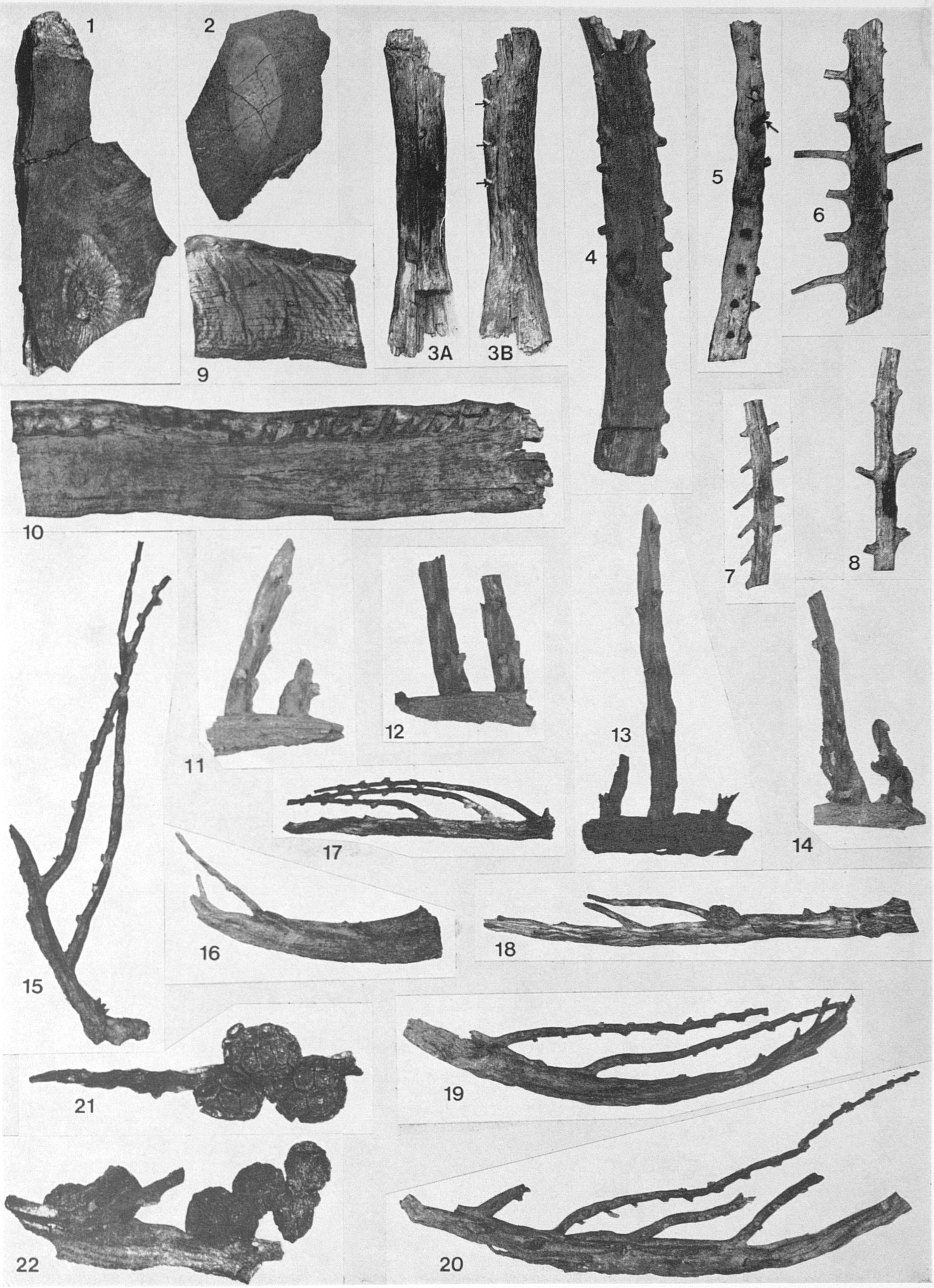
FIG. 9, 10. — Portions of very large primary pinna rachises showing the slightly rugose abaxial surface (below). Fig. 9, no. 1411; Fig. 10, no. 1416. Both ×1.

FIG. 11-14. — Small portions of primary fertile pinnae, each bearing secondary fertile pinnae. (cf. Pl. 2, fig. 3). Fig. 11, no. 576*a*; Fig. 12, no. 576*b*; Fig. 13, no. 576*c*; Fig. 14, no. 747. All ×2.

FIG. 15-20. — Portions of secondary fertile pinnae bearing ultimate rachises (pinnules). Fig. 15, no. 659; Fig. 16, no. 665; Fig. 17, no. 575; Fig. 18, no. 523; Fig. 19, no. 655*a*; Fig. 20, no. 655*b*. All ×2.

FIG. 21. — Ultimate fertile rachis (pinnule) with three soral clusters still attached. No. 540, ×4.

FIG. 22. — Portion of secondary rachis with two ultimate rachises bearing soral clusters. No. 554*a*, ×4.



K. L. ALVIN. — *Weichselia reticulata* (STOKES et WEBB) FONTAINE from the Wealden of Belgium.

EXPLANATION OF PLATE VI.

Weichselia reticulata (STOKES et WEBB) FONTAINE.

A selection of fragments of secondary vegetative pinnae and pinnules. (All photographs by Ch. BOMMER.)

FIG. 1. — A, adaxial; B, abaxial. No. 864. × 9.

FIG. 2. — A, B, side views of pinna fragment. No. 874. ×9.

FIG. 3. — A, B, side views of pinna fragment. No. 878. ×9.

FIG. 4. — Adaxial surface. No. 901. ×9.

FIG. 5. — Adaxial surface. No. 893. ×7½.

FIG. 6. — Adaxial surface. No. 870. ×9.

FIG. 7. — Abaxial surface. No. 891. ×9.

FIG. 8. — Adaxial surface. No. 869. ×7½.

FIG. 9. — Distal end of pinna. Adaxial surface. No. 914. ×9.

FIG. 10. — Side view of pinna fragment showing adaxial surface of pinnules. No. 897. ×9.

FIG. 11. — A, B, side views of pinna fragment showing adaxial (A) and abaxial (B) sides of adjacent pinnules. No. 862. ×9.

FIG. 12. — A, B, side views of pinna fragment showing abaxial (A) and adaxial (B) sides of two pinnules.

FIG. 13. — Abaxial surface of pinna fragment, probably near distal end. No. 900. ×9.

K. L. ALVIN. — *Weichselia reticulata* (Stokes et Webb) Fontaine
from the Wealden of Belgium.

EXPLANATION OF PLATE VII.

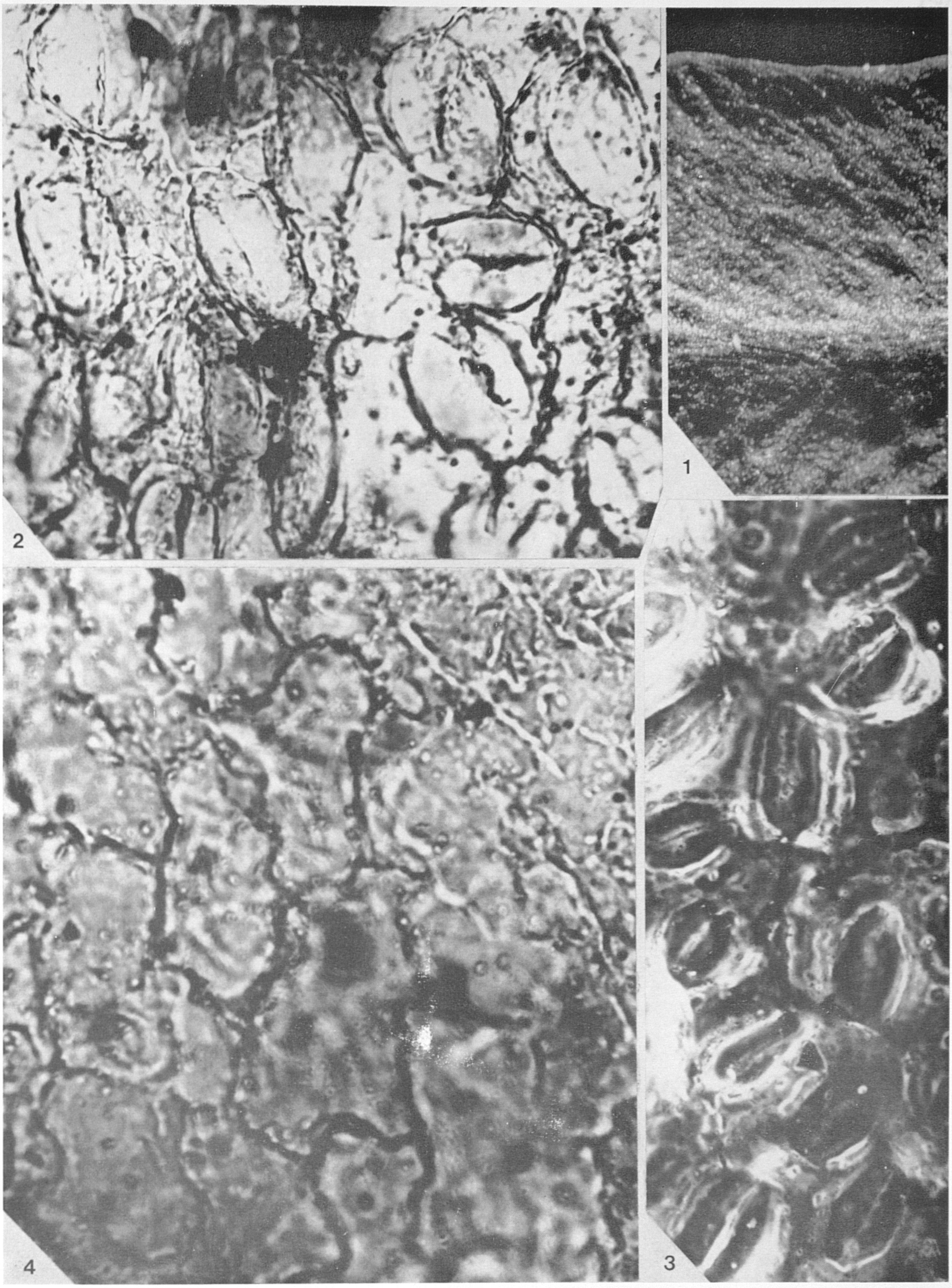
Weichselia reticulata (STOKES et WEBB) FONTAINE.

FIG. 1. — Part of the lower (abaxial) surface of a pinnule showing the prominent raised midrib, the rolled-over margin and the somewhat sunken inter-vein areas with crowded stomata (just visible). ×40.

FIG. 2. — Cuticle from the lower surface showing stomata. Slide N18. ×600.

FIG. 3. — Cuticle from the lower surface, photographed under phase-contrast. Slide N16. ×600.

FIG. 4. — Cuticle from the upper surface. Slide N17. ×950.



K. L. ALVIN. — *Weichselia reticulata* (Stokes et Webb) Fontaine
from the Wealden of Belgium.

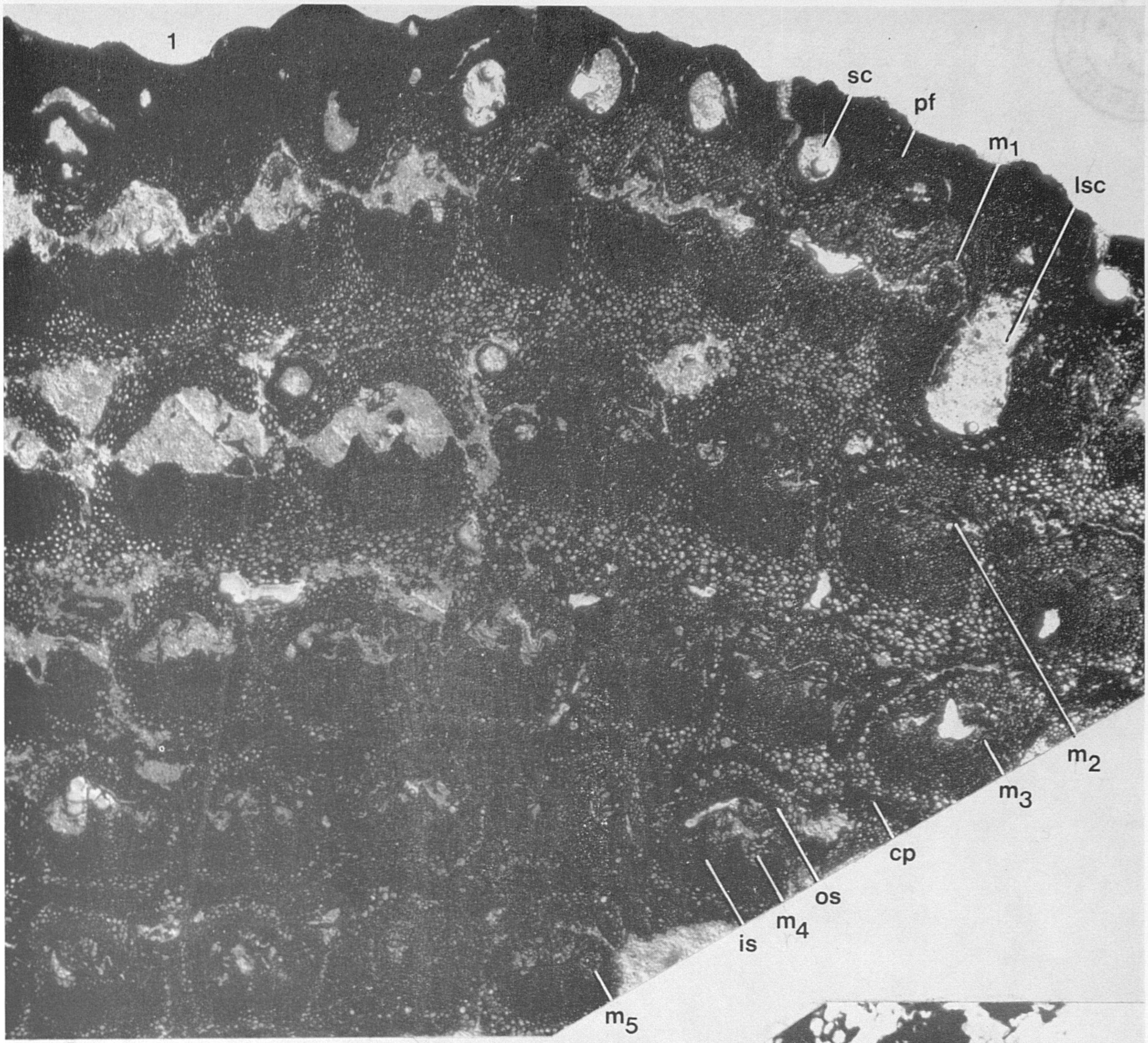
EXPLANATION OF PLATE VIII.

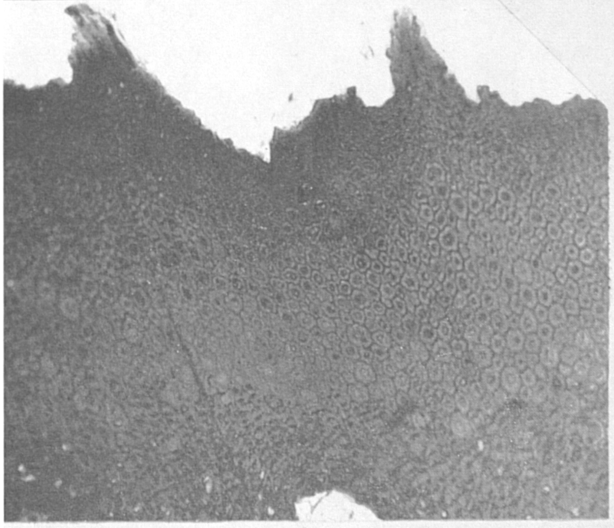
Weichselia reticulata (STOKES et WEBB) FONTAINE.

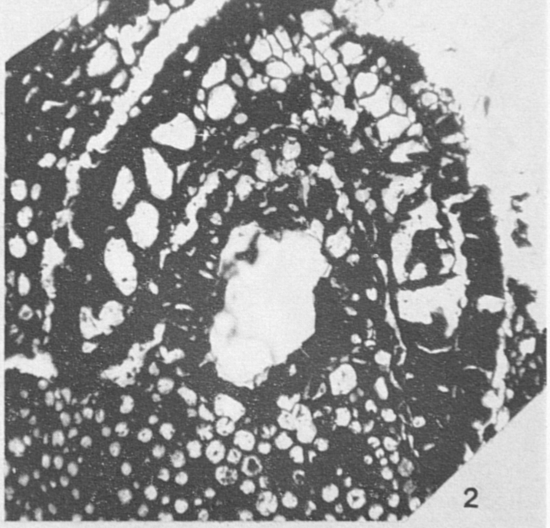
FIG. 1. — Transverse section of a small portion of the stem. m_{1-5}, successive meristele rings; pf, peripheral fibrous tissue; sc, secretory canal; lsc, a large secretory canal protruding into the outermost ring of meristeles; is, inner sheath tissue; os, outer sheath tissue; cp, compressed ground parenchyma between the inner meristeles. Slide N11. × 14.

FIG. 2. — A single meristele showing a prominent cavity in the ground tissue on the concave side. Slide N10. × 80.

FIG. 3. — Small portion of peripheral fibrous tissue in transverse section. Slide N4, 4, 2. × 75.







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EXPLANATION OF PLATE IX.

Weichselia reticulata (Stokes et Webb) Fontaine.

Fig. 1. — Transverse section of a small petiole (specimen no. 1036; Pl. 4, fig. 6) showing about three rings of meristeles and partial confluence of meristeles on the abaxial side. Slide N2/4/3. ×16.

Fig. 2. — Enlargement of a small portion of the same section showing the poor preservation. Possible accessory strands associated with the main meristeles. ×77.

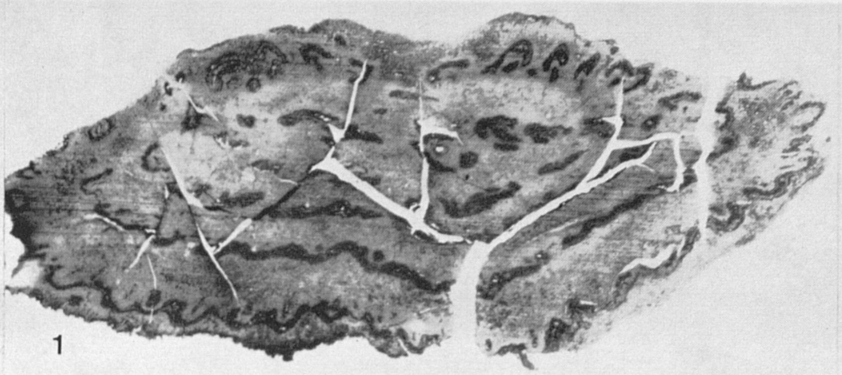
Fig. 3. — Transverse section of a primary vegetative pinna rachis showing about four meristele rings. Specimen no. 1124. Slide N5/2/5. ×20.

Fig. 4. — Transverse section of a secondary vegetative pinna rachis. Preservation poor except for outer fibrous tissue. Slide N9/7/2. ×35.

Fig. 5. — Small portion of another, better preserved secondary pinna rachis, showing two small meristeles with associated ares of rather prominent, palisade-like cells (=? pericycle) Slide N8/7/3. ×80. (Cf. Text-fig. 1 D.)

Fig. 6. — Transverse section of a secondary fertile pinna rachis. Slide N6/6/6. ×30.

Fig. 7. — Transverse section of an ultimate fertile rachis (pinnule) showing the characteristic two arc-shaped meristeles. Slide N7/6/2. ×70.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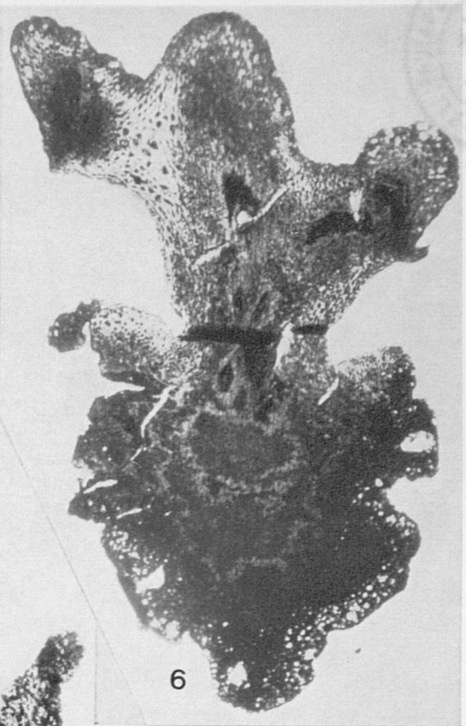
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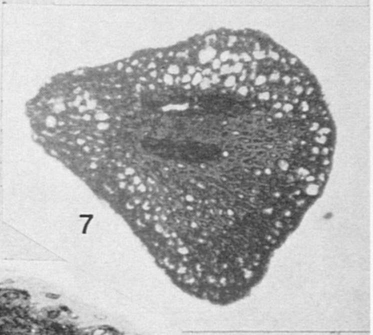
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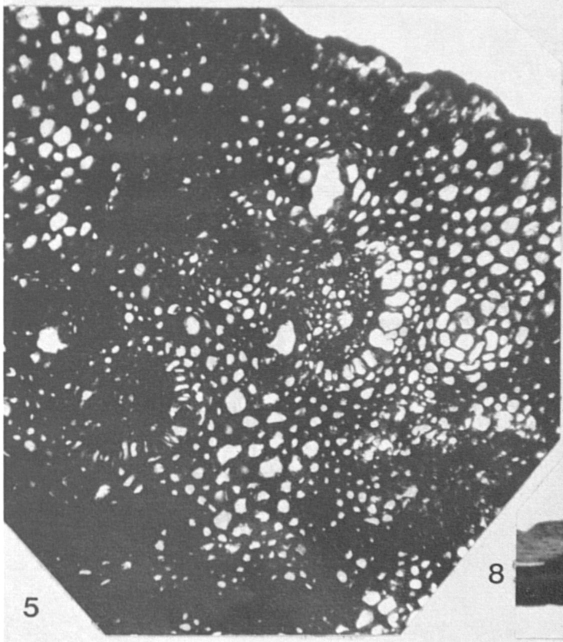
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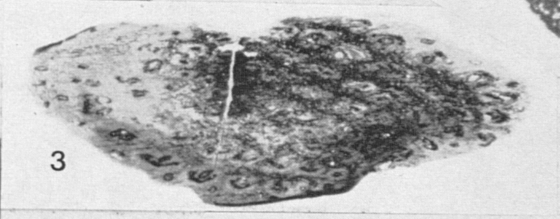
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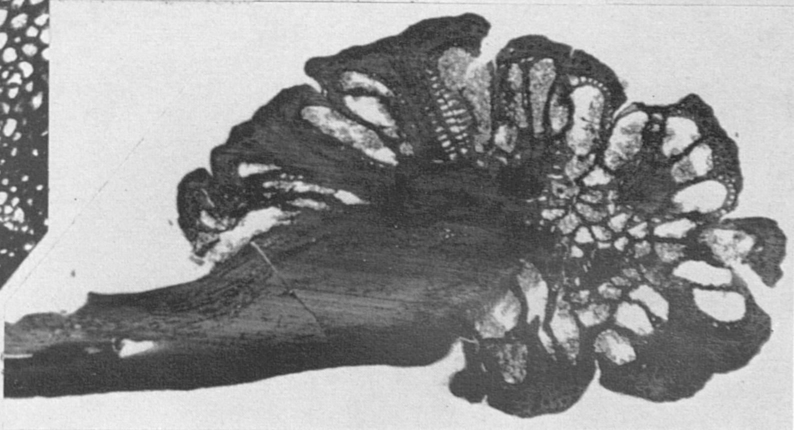
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