

LEAF ANATOMY OF *WEICHSELIA* BASED ON FUSAINIZED MATERIAL

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ABSTRACT. Charred leaf fragments preserved in siltstone show excellent internal structure by SEM. The anatomy presents a high degree of xeromorphism. A number of features, including sunken stomata with paired subsidiary cells, specialized cells of digitate form underlying the upper epidermis and abundant sclereids in the mesophyll, are probably unique among ferns. The significance of the anatomy is discussed in relation to the possible habitat.

THE common and widespread Lower Cretaceous fern *Weichsella reticulata* (Stokes and Webb) Fontaine possesses some unusual morphological and structural characters (Alvin 1968, 1971). Some of these, such as the small, thick pinnules the cuticle of which in well-preserved material can be prepared by oxidative maceration and the sporangia tightly packed beneath thick, sclerotic indusia crowded together into cone-like soral clusters, could be regarded as xeromorphic. Whether the plant was a xerophyte, however, is uncertain, since xeromorphic features are commonly found among plants of wet, especially saline, soils. Gothan (1923), on the basis of what he supposed to be autochthonous specimens preserved in sandstone at Quedlinburg, believed the plant to be an inhabitant of arid dunes. Daber (1968), on the other hand, working on material from the same deposits, believed it grew under conditions of high insolation along river banks near the sea. Its distribution, confined as it apparently is, within palaeolatitudes approximately 30° N. and 30° S. (Barnard 1973), indicates that it was tropical or subtropical.

Although abundant lignitized material from Belgium (Alvin 1971) and occasional petrified major axes from elsewhere, especially North Africa (e.g. Koeniguer 1966) have provided a general picture of the anatomy of the stem, petiole, and rachises, little is known of the internal structure of the vegetative pinnules. The cuticle has revealed the general structure of the epidermis, although there has been considerable variation in the interpretation of the stomata. Florin (1919) and Sukh Dev (1970) described the stoma as being sunken between a pair of subsidiary cells, whereas Reymanówna (1965) and Alvin (1971) failed to see evidence in their cuticle preparations of sunken guard cells and interpreted the pair of superficial cells as guard cells. Although Florin (1919) mentioned having prepared microtomed sections of leaves from Belgium, he did not illustrate the internal anatomy or describe it in any detail. Alvin (1971) failed to obtain worthwhile sections of Belgian leaves.

MATERIAL AND METHODS

In the English Wealden, *Weichselia* is commonly preserved as fragments of fusain (charcoal) in a sandy, often current-bedded matrix. Such material, which forms the basis of this study, was collected from a lens of siltstone at Shepherd's Chine, half a mile north-west of Atherfield Point, Isle of Wight.

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The matrix is a fairly uniform, pale grey, coarse siltstone (grain size *c.* 0.03 mm), somewhat unevenly bedded, with occasional small pockets of finer sediment. It contains numerous fragments of *Weichselia* representing pinnules, portions of pinnae with several pinnules attached, naked rachises and larger, usually striated pieces of fusain which may represent fragments of the more massive organs of the plant (stems, petioles, or main pinna rachises). Plate 87, fig. 1 shows a typical sample of material. Nearly all of the plant fragments appear to represent *Weichselia*. The only other plants occasionally present are *Phlebopteris dunkeri* (Schenk) Schenk (sterile and fertile pinnule fragments) and ?*Cladophlebis* sp. (sterile pinnules). Bulk maceration of a small sample of matrix yielded one fragment probably representing *Ruffordia goepperti* (Dunker) Seward.

All but very few of the plant fragments present are charred; they are extremely brittle and smear the fingers at a light touch. Occasionally present (estimated at less than 1% of the total) are non-charred or only partly charred pieces. The occurrence of such partially charred fragments provides evidence that the fusain represents true charcoal and has not been produced by a diagenetic process. Some of the non-charred (lignitized) *Weichselia* pinnules have been softened in alcoholic KOH solution, embedded, and sectioned. They are poorly preserved (Pl. 87, fig. 3), but what structure they show assists interpretation of the scanning electron microscope pictures of fusainized material.

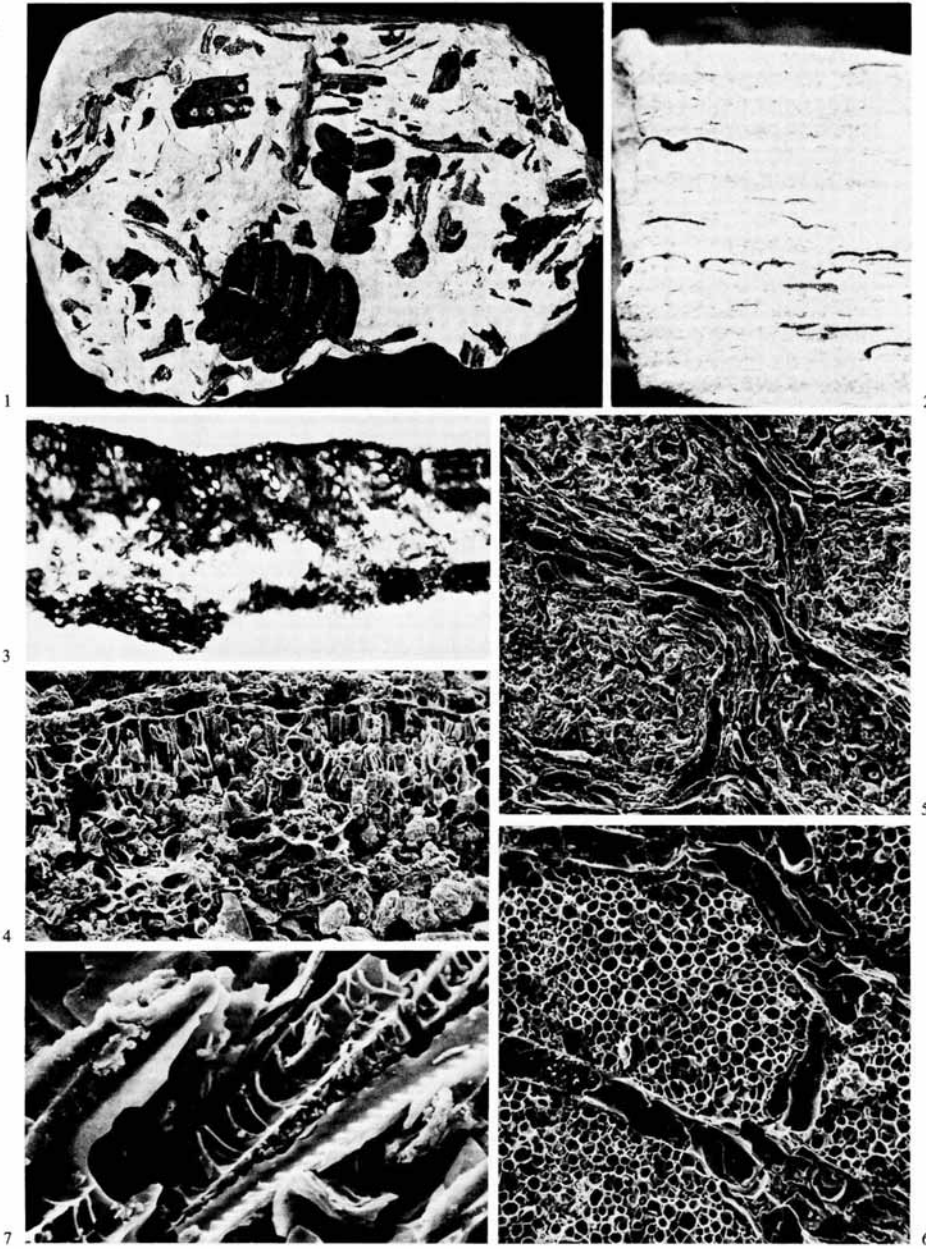
Preparation of fusainized material for SEM is relatively simple. Since most of the pinnules and pinna fragments lie with their lamina in the bedding plane, cleavage of the matrix ruptures them in the plane of the lamina. Hardly ever does the pinnule separate them from the matrix at the surface. Freshly fractured pinnules may be mounted and viewed with no further treatment other than routine metal coating. Since fracture of pinnules usually occurs in the same plane, namely through the middle of the mesophyll and vein system, other levels of section parallel to the lamina surface (i.e. nearer to the upper or lower epidermis) have effectively been obtained by gently brushing away the charcoal with a fine camel-hair brush. Such brushed specimens are improved by immersing them subsequently in a beaker of distilled water in which an ultrasonic probe is inserted for about 10 seconds.

Cross-sections of pinnules are obtained by breaking samples of matrix across the bedding plane or by grinding in this plane on fine sandpaper. Transverse sections of pinnules may be recognized by their shape (Pl. 87, fig. 2). Small slabs of matrix

EXPLANATION OF PLATE 87

(Figs. 4-7 are scanning electron photomicrographs.)

Figs. 1-7. *Weichselia*. 1, a typical sample of material showing fragments of pinnae and pinnules with, near the top left, a piece of a fertile pinnule of *Phlebopteris dunkeri*, $\times 2$. 2, a block ground at right-angles to the bedding plane showing cross-sectioned pinnules, $\times 4$. 3, light microscope photograph of part of a microtomed section of a lignitized pinnule, $\times 75$. 4, part of a cross-section of a pinnule. A vein is seen slightly right of centre and another near the left-hand edge, $\times 176$. 5, part of a pinnule fractured parallel to the surface through the spongy mesophyll showing the rather broad vein sheaths, $\times 168$. 6, part of a pinnule fractured parallel to the surface and brushed towards the upper side showing the regular, palisade-like cells and the vein sheaths, $\times 164$. 7, part of a vein with tracheids and associated ruptured cells, $\times 1600$.



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on which such sections are exposed are stuck to the microscope stub and washed by brief ultrasonic treatment as before.

The outer surface of the pinnule has been observed from specimens freed from the matrix in hydrofluoric acid.

All specimens for SEM observation are cemented to the stub with 'Durofix' and coated with gold-palladium.

RESULTS

Interpretation of scanning electron micrographs of charcoal surfaces presents certain difficulties. The image obtained, which is very different from that of a sectioned tissue viewed in the light microscope, represents a view of the surface of the often very irregularly fractured cells and tissues. Some parts of this surface will represent the inside of cells, some the outside, either where natural intercellular spaces occur or perhaps where abutting cells have separated along the plane of the middle lamella, and some the fractured cell walls. Further difficulties may arise from various distortions likely to have been produced (*a*) by charring, (*b*) by compression, and (*c*) by precipitation of minerals such as iron pyrites in the tissues. Harris (1957) has made some reference to the distortion in plant tissues produced by charring: the distortion in wood is unpredictable, but frequently the rays become distended into gaping holes. There is no evidence of gross distortion of this kind in the *Weichselia* leaves, but some of the cell walls appear to have been structurally altered. Compression seems to have resulted in a variable degree of shattering and compaction of the tissues, chiefly in the region of the spongy mesophyll. Precipitation of iron pyrites in the form of small spherical masses is frequent, especially again in the spongy mesophyll, and in some specimens this is accompanied by gross disruption of the tissues.

Morphology and surface features

In shape and size the pinnules show a similar range of variation to that shown by material from Belgium preserved as lignite (Alvin 1971).

The upper surface is smooth and generally convex, the convexity increasing towards the thick, somewhat rolled-over margin. The midrib is sometimes marked by a shallow furrow, especially towards the base of the pinnule. The lower surface is more or less scrobiculate, with the veins represented by low ridges and the inter-vein areas by shallow depressions.

A remarkably conspicuous feature of the lower surface is the large, crowded, and somewhat bulging stomatal subsidiary cells (Pl. 89, fig. 1). As much as about 40% of the area of the lower surface is occupied by these cells which are 50–85 μm in length. The cells of each pair are either in contact along their length, or, more frequently, separated by a narrow, slit-shaped space. At first it was thought that these cells were the guard cells, but views of the inside of the epidermis have made it clear that the true guard cells are considerably smaller and sunken below the leaf surface. The subsidiary cell pairs are oriented at random and almost uniformly scattered so that the veins are not clearly marked by their distribution. The ordinary epidermal cells are not distinguishable in the surface relief, but occasionally there occur small, round, somewhat depressed areas around which subsidiary cell pairs often tend to

radiate (Pl. 89, fig. 1, above and slightly right of centre). These areas are believed to be equivalent to the 'papillae' mentioned by Reymanówna (1965) and the 'small round cells' noted in the cuticle by Alvin (1971). Diminutive subsidiary cell pairs about half the size of normal ones also occur (Pl. 89, fig. 1, bottom right-hand corner).

Internal structure

The leaflet fractured parallel to the surface always shows a conspicuous vein network (Pl. 87, figs. 5, 6). The veins consist chiefly of thick-walled cells elongated in the direction of the vein. This fibre-like vein sheath tissue is seen in cross fracture (Pl. 87, fig. 4) to extend above and below the vein to both epidermises. In sections of lignitized leaves (Pl. 87, fig. 3), it is only seen as blocks of tissue beneath the epidermis, perhaps because here it was thicker walled and therefore more durable than around the veins nearer the middle of the leaf. In fractures parallel to the surface the tissue always appears broader in the spongy mesophyll region and to consist of narrower cells (Pl. 87, fig. 5) than nearer the upper epidermis where there are typically only one or two rows of broader elements (Pl. 87, fig. 6). In the spongy mesophyll region there is some gradation between the fibrous sheath tissue and the mesophyll. Sheath cells often show conspicuous pit-like markings under high magnification (Pl. 88, fig. 7); it is possible that some of the sheath cells functioned as transfusion elements.

The vascular bundle lies within the sheath where this is broadest, at or just below the middle of the leaf. It is indicated by a small core of usually shattered, thin-walled cells in which can sometimes be seen tracheids (Pl. 87, fig. 7). The tracheids are scalariform, scalariform-reticulate, or sometimes annular. Very beautifully preserved scalariform tracheids have been seen in the midvein of pinnules and in pinna rachises (Pl. 89, fig. 6). In some of the thin-walled elements associated with the tracheids in these stronger vascular strands, a wall sculpturing resembling sieve areas can sometimes be seen (Pl. 89, fig. 6, top left-hand corner).

The mesophyll is clearly differentiated into two regions. Underlying the upper epidermis is a palisade-like region, well seen in cross fractures (Pl. 87, fig. 4). Below this, extending to the lower epidermis and occupying rather more than half the thickness of the leaf is the spongy mesophyll. There is no very clear demarcation line between the two regions; they intergrade by one or two rows of rather compactly arranged rectangular cells.

A section parallel to the surface through the palisade-like region (Pl. 87, fig. 6; Pl. 88, fig. 3) shows rather regular, cylindrical elements in cross-section with triangular or polygonal intercellular spaces. Nearer the upper epidermis (Pl. 88, fig. 2, right-hand side) the intercellular spaces become smaller and eventually the cylindrical elements unite in groups of four to six to form large, lobed cells somewhat resembling epidermal cells with sinuous anticlinal walls (Pl. 88, fig. 2). At first it was thought that this level did indeed represent the epidermis; however, there is an absence of any periclinal wall separating the lobed cells from their cylindrical, palisade-like extensions. Further, the connections between adjacent palisade-like elements can also be seen in cross fractures (Pl. 88, fig. 1, top right). The true epidermis, consisting of large cells which are conspicuous in cross fractures, can also be seen in Plate 88, fig. 4, where, at the top of the photograph, the sub-epidermal layer has been completely removed by the brushing treatment. Hence, it emerges that the sub-epidermal layer

consists of large digitate cells each with four to six digits arising from the lobed head and oriented towards the interior of the leaf. The possible function of these cells is discussed later.

The spongy mesophyll consists mainly of irregular, thin-walled cells with small pits (Pl. 89, fig. 2). Also present, often abundantly, scattered in the mesophyll are sclereids or stone-cells. These are often conspicuous in sections of lignitic leaves (Pl. 88, fig. 5), but only seldom are they seen in the SEM, probably because they do not easily fracture and cannot be recognized from a surface view of the cell. Two probable stone-cells are seen at the bottom of Plate 88, fig. 1, and one of these is shown enlarged in Plate 88, fig. 6. The frothy appearance of the wall may have been produced by charring.

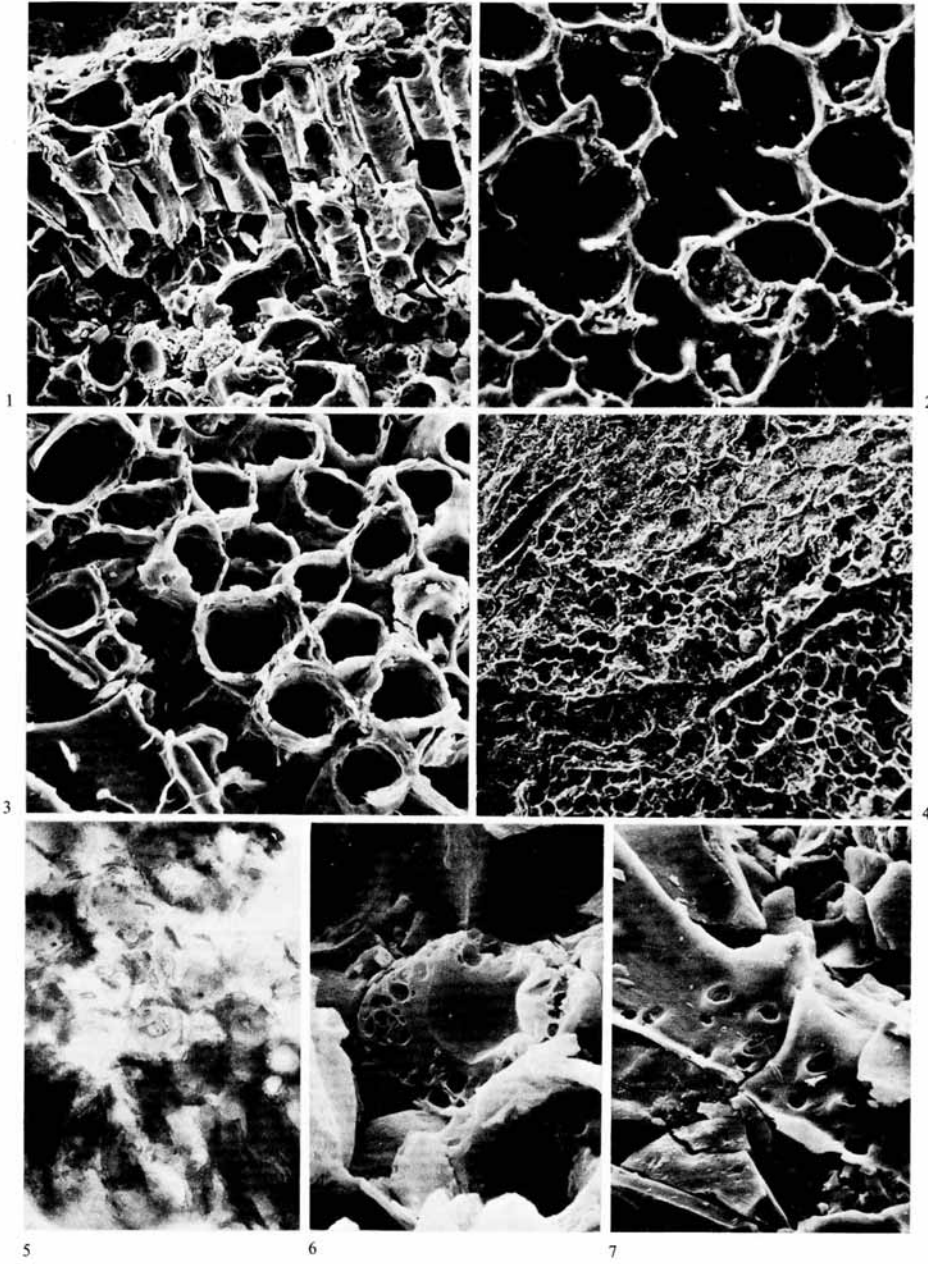
Specimens cleaved in the plane of the lamina and brushed towards the lower epidermis show spongy mesophyll between the veins and, if brushed sufficiently, the stomata and lower epidermis from the inside. Plate 89, fig. 2, shows the pair of intact guard cells of a stoma situated in a space in the spongy mesophyll presumably representing the sub-stomatal air chamber. In more vigorously brushed specimens the spongy mesophyll is often removed completely and the guard cells broken open or removed. Plate 89, fig. 3, shows a stoma in which only the outer periclinal walls of the guard cells are present; surrounding these can be seen the damaged walls of the subsidiary cells. At the centre, two pairs of lips separating narrow, slit-like openings are visible: the upper (inner), wider opening (*c.* 3 mm wide in the photograph) represents the stomatal aperture itself (*i.e.* between the lips of the guard cells); the lower (outer) and narrower (*c.* 1 mm wide in the photograph) opening represents the space between the subsidiary cells. In Plate 89, fig. 4, the specimen has been brushed so as to remove not only the spongy mesophyll and guard cells, but also the inner and, in some cases, the outer walls of the subsidiary cells; where the outer walls have been removed, the matrix can be seen.

Unfortunately, no satisfactory cross-sections of stomata have been obtained, but this interpretation of the stomatal organization is in general agreement with that of Florin (1919) and Sukh Dev (1970) both of whom based their results mainly on cuticle preparations. However, both of these authors described the stomatal pit as wide. In the cuticle shown in Plate 89, fig. 5, prepared from a lignitic pinnule, the large, somewhat granular cells undoubtedly represent the subsidiary cells. If the small,

EXPLANATION OF PLATE 88

(All except fig. 5 are scanning electron photomicrographs.)

Figs. 1-7. *Weichselia*. 1, detail from a section similar to that in Plate 87, fig. 4 showing the upper epidermis, the palisade-like sub-epidermal layer, part of the spongy mesophyll with two probable stone-cells; (the one near the bottom right is shown enlarged in fig. 6), $\times 480$. 2, part of a specimen prepared in the same way as that in Plate 87, fig. 6 showing, on the right, palisade-like digits of the sub-epidermal layer and, at the centre and left, the lobed end portions of these cells, $\times 920$. 3, detail from a similar section to that shown in Plate 87, fig. 6, $\times 896$. 4, a low-power view of the same specimen as in fig. 2 showing three levels of section parallel to the surface: at the bottom, digits of the sub-epidermal layer in cross-section; left of centre, lobed heads of these cells (as in fig. 2); top, the epidermis. Note that in the sub-epidermal layer, fibres are seen marking the course of veins, $\times 224$. 5, light microscope photograph from a sectioned lignitized leaf showing stone-cells in the mesophyll region, $\times 380$. 6, probable fractured stone-cell, $\times 1600$. 7, detail of vein sheath cells showing pit-like structures, $\times 1840$.



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clearer areas between the subsidiary cell pairs were interpreted as guard cells, this would suggest a wide stomatal pit. If, however, the clear areas represent rather the cutinized anticlinal walls of the mouth of the stomatal pit, the guard cells not being represented due to insufficient cutinization, this would accord with the SEM view. Narrowing of the stomatal pit has not been produced by charring, for the external appearance in the SEM of the stoma of a lignitic leaf is the same as that of a fusinized specimen.

DISCUSSION

Weichselia presents a leaf anatomy unique among known ferns. The reproductive structures as well as certain aspects of morphology and vascular anatomy suggest an affinity with Matoniaceae (Alvin 1971). The pinnule anatomy of the living *Matonia pectinata* R. Br. has been examined, but shows little resemblance to that of *Weichselia*: it shares only one character, namely, the presence of vein sheath tissue extending to the epidermis.

Especially noteworthy are the stomata and the cells underlying the upper epidermis. The stoma, with its pair of specialized subsidiary cells has, according to van Cotthem's (1970) extensive studies, no parallel among ferns. It is, however, remarkably similar to that of *Equisetum*, where, as in *Weichselia*, the subsidiary cells form a narrow pit above the sunken guard cells (Hauke 1957; Page 1972). There is also a general similarity to the Bennettitalean stoma and that of the living *Welwitschia* among gymnosperms.

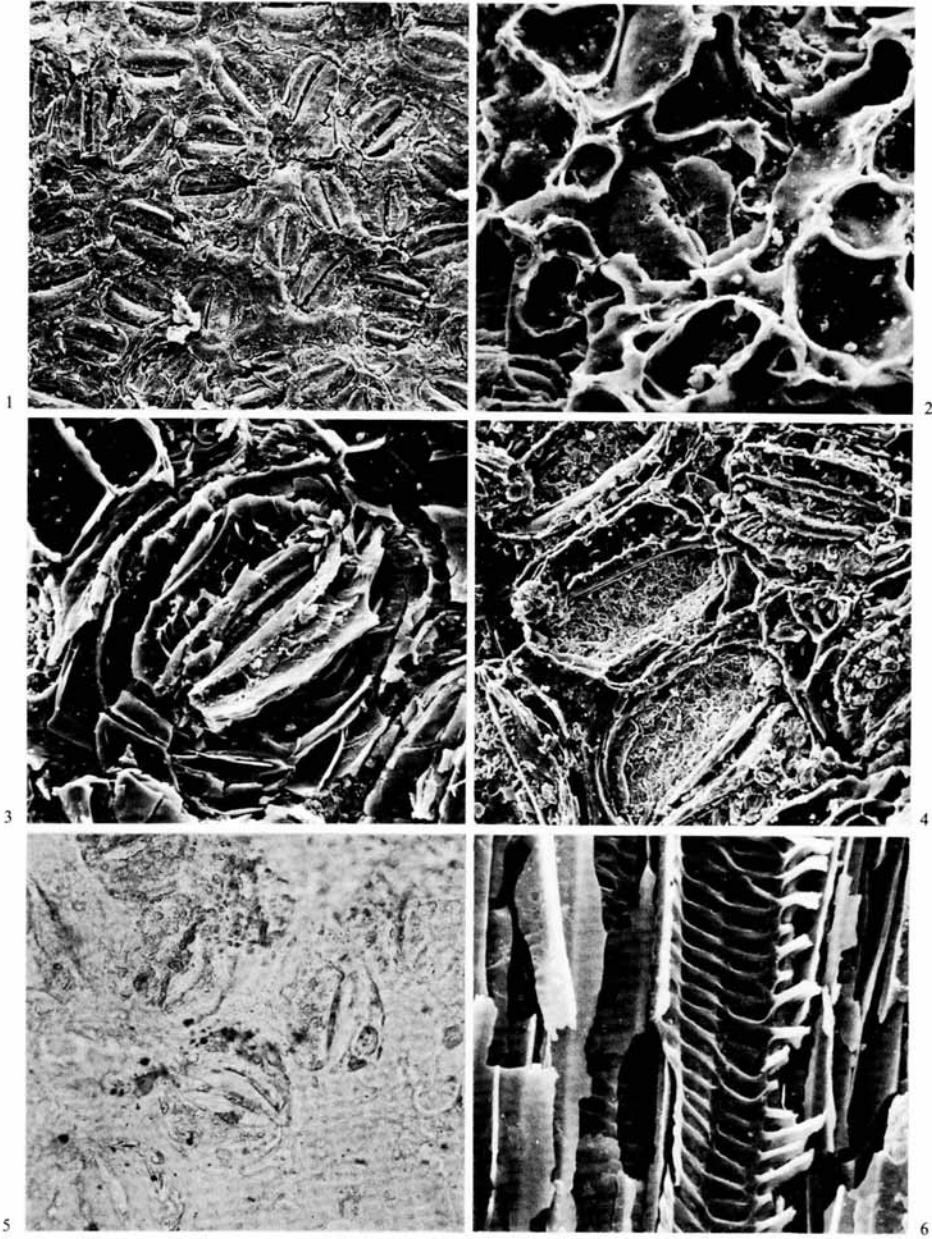
The digitate sub-epidermal cells suggest another highly specialized feature. The presence of abundant intercellular spaces between the digits and the absence of noticeably thicker walls than in the spongy mesophyll cells point perhaps to a photosynthetic function. On the other hand, the somewhat prominent pitting might suggest a water-storage function. A sub-epidermal water-storage layer has been reported in the xerophytic fern *Pyrrosia lingua* (Thunb.) Farwell by Hungerbühler (1957). The upper epidermis in *Weichselia* is itself quite large-celled as seen in cross fractures (Pl. 88, fig. 1). One might speculate that this had a water-storage function.

Apart from the sunken stomata and the possibility of the presence of a water-storage system, some of the other characters may also be regarded as xeromorphic, notably: (a) the thickness of the lamina (up to about 0.5 mm); (b) the presence of

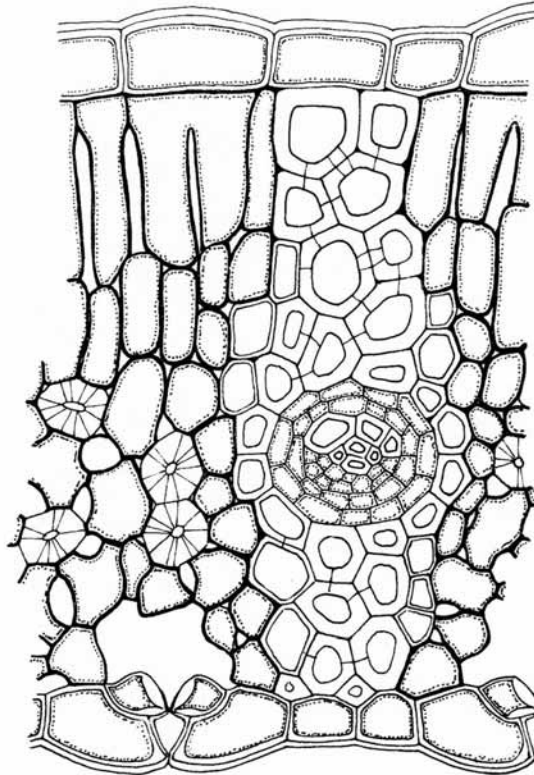
EXPLANATION OF PLATE 89

(All except fig. 5 are scanning electron photomicrographs.)

Figs. 1-6. *Weichselia*. 1, part of the lower surface of the pinnule, $\times 160$. 2, specimen fractured parallel to the surface and brushed towards the lower side showing spongy mesophyll cells and a stoma from the inside, $\times 420$. 3, specimen brushed to lower epidermis showing a stoma the guard cells of which are ruptured to expose the outer periclinal walls; surrounding them are seen the somewhat broken walls of the subsidiary cells, $\times 840$. 4, specimen brushed still lower showing the epidermal cells and stomatal subsidiary cells some of which have had their outer walls removed thus exposing the matrix, $\times 464$. 5, light microscope photograph of the lower cuticle prepared from a lignitized leaf, $\times 380$. 6, vascular tissue in a pinna rachis, $\times 1600$.



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TEXT-FIG. 1. Proposed reconstruction of the pinnule lamina as seen in transverse section.

a cuticle resistant to oxidative maceration; (c) abundant fibrous tissue round the veins extending to the upper and lower epidermis; (d) the presence of sclereids in the mesophyll.

Xeromorphic features do not occur commonly among ferns although, as Hungerbühler (1957) has shown, certain characters comparable with some generally regarded as xeromorphic among angiosperms do occur. Thus, *Ceterach officinarum* DC., *Cheilanthes gracillima* Eaton, *C. marantae* (L.) Domin, and *Doryopteris ornithopus* (Mett.) J. Sm. have thick leaves with a double palisade. *Pellaea ternifolia* (Cav.) Link and *Anemia millefolia* Gardn. ex Pressl have fibrous tissue above and below the main veins. A hypodermis is reported in *Elaphoglossum latifolium* (Swartz) J. Sm. *Pyrrosia confluens* (R. Br.) Ching has sunken stomata and in a number of ferns the stomata are protected by inrolling of the margin (e.g. *Cheilanthes* spp. and *Pellaea* spp.) or by the presence of persistent scales or hairs on the lower surface (e.g. *Ceterach* and

Cheilanthes spp.). Most of these ferns grow in habitats subject to periods of drought, and the xeromorphic features may be assumed to be physiologically advantageous under these conditions.

Among angiosperms, xeromorphic characters may occur in plants of wet soils, and as a wet maritime habitat has been suggested for *Weichselia* by Daber (1968), the leaf anatomy of *Acrostichum danaeifolium* Langsd. et Fisch. and *Blechnum indicum* Burm. has been examined. Both of these ferns grow in tropical brackish water swamps often under conditions of high insolation, but neither show any notable xeromorphic characters.

The combination in *Weichselia* of a number of xeromorphic features, some developed to an extreme degree (e.g. the cuticle, fibrous tissues, and sunken stomata) suggests strongly that the plant grew in a habitat subject to periods of extreme drought. Only comparatively rarely do other plants occur in close association with the fossil remains of *Weichselia*; certain Matoniaceae are probably the most frequent associates, but are seldom present in any quantity. It may therefore be conjectured that *Weichselia* dominated the community in which it grew. This is consistent with the idea that it was adapted to life in an extreme environment to which few plants are likely to have been suited.

Daber's (1968) conclusion that *Weichselia* grew along river banks close to the sea was based on his presumed *in situ* specimens found just above dark humic layers in sandstones believed to have been laid down under fluvial conditions near the coast. The presumed rooted specimens, however, are almost certainly only the heads of large petioles (Alvin 1971), and therefore not indicative of *in situ* preservation. On the other hand, the Quedlinburg specimens of fronds and probable stems (= *Stiehleria* Daber) are impressively large, and it therefore seems probable that the remains had not been transported far. Thus they may have been preserved as the rivers, perhaps in times of flood, cut through stands of *Weichselia* growing in otherwise arid conditions. Large specimens of *Weichselia* are only comparatively rarely encountered, and the Quedlinburg conditions of preservation may therefore have been exceptional. Much more commonly the plant is preserved as small fragments, often in the charred condition. This hardly suggests that it was a plant of river banks, but rather that it grew in areas somewhat remote from sites of deposition, and was only brought down at times of flood. The frequency with which remains occur charred is consistent with the idea that the community was at times subjected to dessication when it would have been especially vulnerable to the spread of fire.

Concerning proximity to the sea, *Weichselia* remains are nearly always found in freshwater deposits. Only rarely are fragments found in marine sediments (e.g. sandstones in the Aptian of England). This does not suggest that the plant was especially associated with maritime conditions.

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