TYGE W. BÖCHER & OLE B. LYSHEDE

ANATOMICAL STUDIES IN XEROPHYTIC APOPHYLLOUS PLANTS

II. ADDITIONAL SPECIES FROM SOUTH AMERICAN SHRUB STEPPES

Det Kongelige Danske Videnskabernes Selskab
Biologiske Skrifter 18, 4

Kommissionær: Munksgaard
København 1972

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Abstract

Almost twenty South American species ascribed to the apophyllous life form have been investigated anatomically with special reference to the structure of epidermis. The species can be divided into three anatomical groups, each representing a subtype of the life form in question: The species are treated separately as a series of short monographs. The discussion and the concluding remarks on p. 121 concentrate upon the xeromorphic characters. Regarding the non-xeromorphic characters the reader is referred to a subject index on p. 133. In the conclusion special attention is given to wax deposits, micro-channels in outer epidermal walls, the structure of the cuticular layer, the occurrence of shelters outside stomatal front cavities, the structure of the front cavities, as well as the reduction in distance from the vascular to the photosynthetic tissues, the latter mostly being composed of radiating palisade cells. A final part of the discussion concerns the evolutionary trends leading to stem-assimilatory xerophilous species. The three subtypes of apophyllous plants are represented in two larger systematic groups viz. *Fabales* and *Asterales*. The anatomical differences between the two family representatives of the three subtypes are significant, generally speaking, but the differences between the three subtype representatives from the same systematic group are equally large. A number of characters probably substitute one another so that the same level of adaptation is reached by different character combinations. Some characters, however, seem particularly important, these being common to a number of plant species, and thus highly contributing to a characterization of a life form.

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1. Introduction

Our second paper deals with a number of South American apophyllous or stem-assimilatory species of which material was collected for anatomical studies by the senior author during his journeys in Western Argentina in 1955–56, see Böcher, Hjerting & Rahn 1963, 1968, and 1972. Additional material was collected later by Hjerting and Rahn. The main purpose of gathering the materials and doing the anatomical studies was to find similarities as well as dissimilarities in a number of species which morphologically belong to the same life form. The species belong to families in which most members are foliate. As a result of a convergent evolution, however, some species of widely different origin have approached one another closely in vegetative morphological characters. Accordingly an important question is to find out to what extent the anatomical characters are the results of the same convergent trends and how much anatomical family characters are maintained in the apophyllous species.

The word aphyllous is used by many authors which thus ignore the fact that aphyllous plants (apart from *Rhynia* etc.) either bear reduced scale leaves or small foliage leaves which are shed early. The word apophyllous expresses "away from leaves" e.g. that the plants during evolution have reduced their foliage leaves. Unfortunately, the term "apophyllous" has also been used about perianth leaves.

In Part II the same principles are followed as in Part I. Thus we have tried to make a short monograph of each species and to deduce a conclusion from a comparison of the monographs of the species.

A deviation from the earlier treatise is the use of interference contrast and scanning electron microscopy. The SEM photos were taken by Ole Lyshede in cooperation with Annelise Nørgaard, at the Mineralogical Museum of the University of Copenhagen. Most slides used for light microscopy were prepared by Mrs. Else Marie Graves Petersen, who took great interest in this work. The slides were studied and discussed by both authors, but the compilation of the text and most of the photographs are due to the senior author. Both of us wish to express our sincere thanks to the two technicians mentioned above and also to Mr. Sv. Å. Svendsen who produced the magnifications of the photos with great care and skill, and to Mrs. Kirsten Pedersen who assisted in revising the English translation.

In Part I pp. 40–41 a suggested subdivision of apophyllous species was briefly discussed. Two main subtypes were discussed viz. the terete and the furrowed one. A similar division has been followed in the present text, where, however, also some other criteria are used e.g. the position of sclerenchymatous areas (fiber strands), hair cover etc.

2. Species with a continuous cylindrical chlorenchyma. No fiber strands reaching the peripheral layers.

To this category belong *Monttea aphylla*, *Bulnesia retama*, and *Bredemeyera colletioides* mentioned in Part I. These three species are members of the *Scrophulariaceae*, the *Zygophyllaceae*, and the *Polygalaceae*, respectively. In Part II this group will contain species from *Euphorbiaceae*, *Caesalpiniaceae*, *Rhamnaceae*, and *Solanaceae*. All have a continuous photosynthetic outer cortex tissue. Fiber strands may be present (e.g. in *Cassia*), but such strands do not reach the epidermis or hypodermis. Most species are glabrous or with very few trichomes. Only *Fabiana* (*Solanaceae*) has a dense cover of glandular hairs.

Stillingia patagonica (Speg.) Pax & Hoffm. (Euphorbiaceae).

Material: W. Argentina, the Atuel Valley. Arroyo Blanco, 1800 m. above sea level. Böcher, Hjerting & Rahn No. 708, Oct. 31, 1955.

Occurrence and morphology

A very branched shrub, 0.5–1 m. tall with Patagonian distribution. It is abundant in several localities in the lower part of the Atuel Valley in altitudes ranging between 1700 and 2000 m. above sea level, cp. Fig. 1 a. Details about its choice of habitat here appear from Böcher, Hjerting & Rahn 1971. Near la Faja and Arroyo de los Papagayos north of the Atuel Valley it grew abundantly on the level plateau, in an altitude of 1900–2000 m. together with *Neosparton aphyllum* and *Fabiana viscosa*, thus in a vegetation composed of three apophyllous shrubs.

Lateral branches are supported by a persistent leaf base. Below they carry a few scale leaves. These are followed by narrow assimilatory leaves which at the base of the blades have two opposite globular extra-floral nectaries. The leaves are probably to a large extent shed when the flowering is over. The plants on Fig. 1 a from early spring had very few leaves left.

Leaf anatomy

The blades are about 1–2 mm broad and about 8–10 mm long and have usually three strong parallel vascular bundles. Stomata and palisade tissue are found on both sides. Yet, the leaves are not typically isolateral. The upper side is slightly concave, the lower convex. The epidermal cells on the upper side and along the margins have parallel running longitudinal cuticular ridges (Plate II a). These structures are lacking on the underside. A hypodermis is present on both sides, but is better developed on the underside. In the middle of the leaf, between the vascular bundles and the palisade tissue of the underside, an interesting complex laticiferous tissue occurs. It is composed of non-articulated laticifers and long parenchyma cells, both with their long axis parallel to the veins (Plate II a). The phloem occupies a layer between the xylem and this laticiferous tissue. The stomata are all provided with cutinized outer ledges and

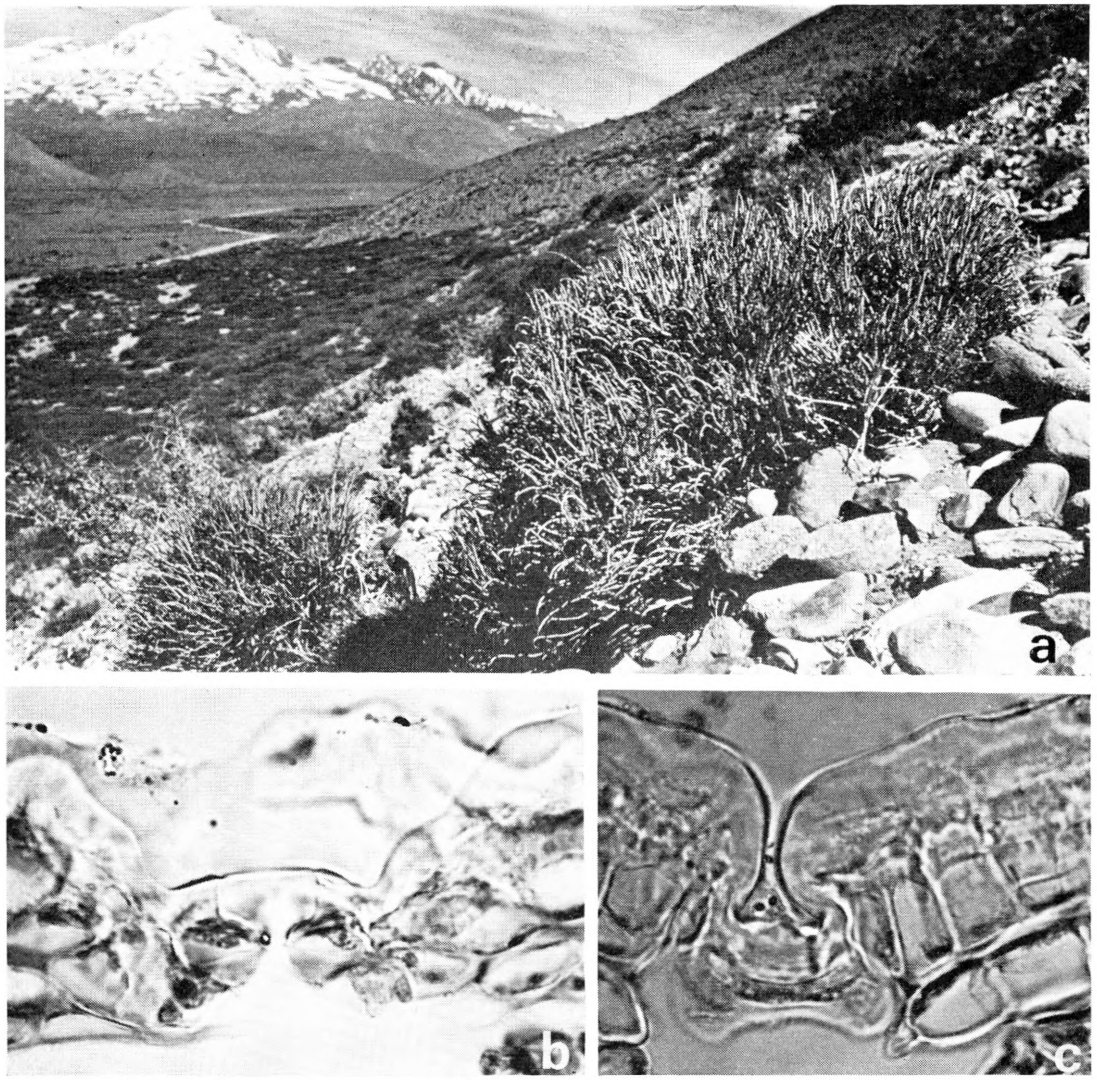


Fig. 1. *Stillingia patagonica* on stony slope in the lower part of the Atuel valley, W. Argentina. Below stomatal pore from stem in transverse section (on the left) and longitudinal section showing narrow entrance to the epistomatal cavity (× 640).

front cavities, but they are not sunken. The cuticular layer of the epidermis cells is well developed but not very thick and almost without cuticular flanges over transverse walls.

Extra-floral nectaries. The two opposite nectaria arise as invaginations from the leaf margins (Fig. 2). The epidermis lining the invaginated cavities consists of elongate secretory palisade cells with thick cutinized outer walls. Also the upper part of

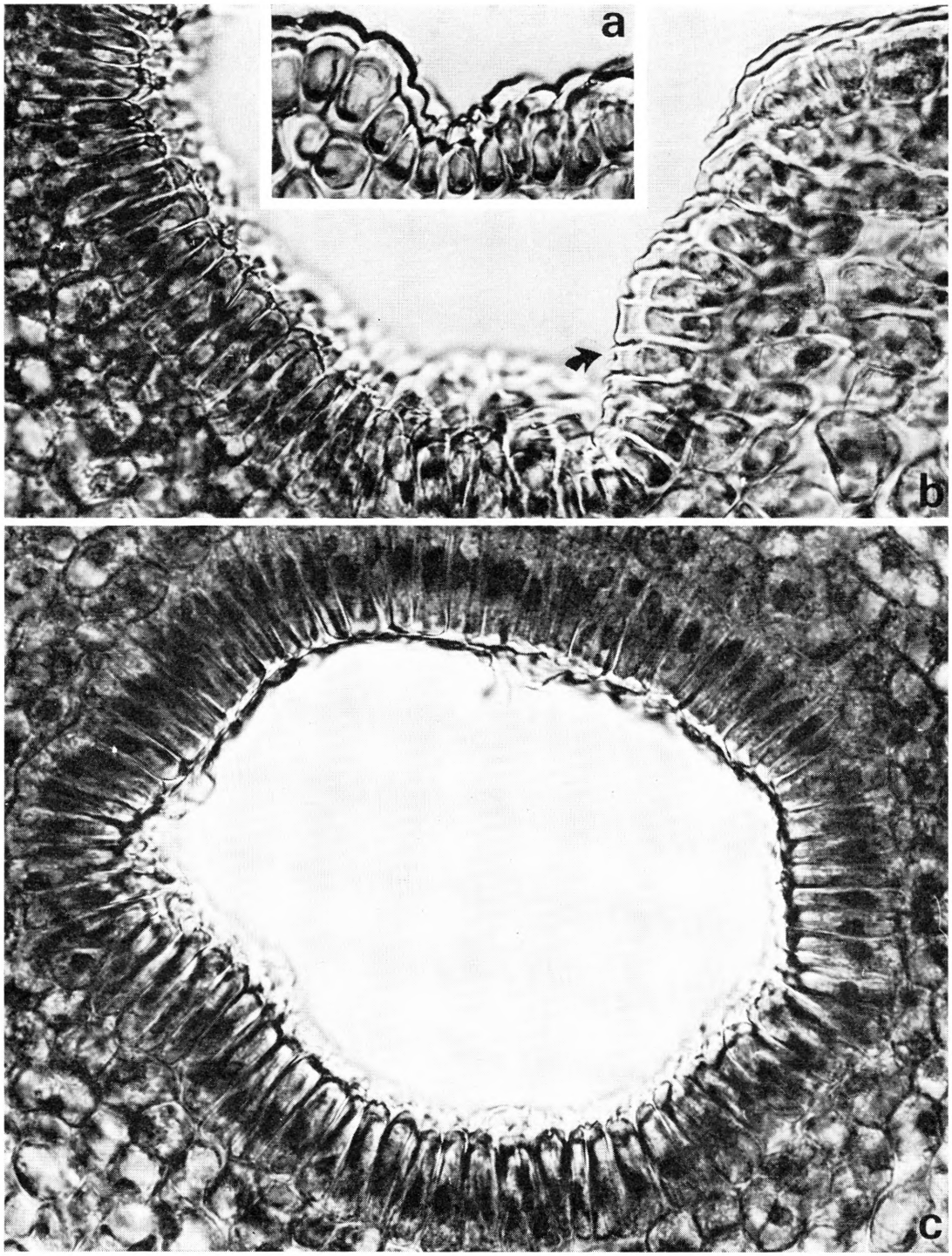


Fig. 2. *Stillingia patagonica*. Extra-floral nectarium in base of leaf blade. a. Invagination at the leaf margin. — b. Invagination; marginal area, from the right side towards the left the transition from normal epidermis cells to secretory cells can be followed. Note cuticular folds and beaks at arrow. — c. Cavity in nectarium surrounded by secretory palisade cells, cp. Plate II (× 500).

the transverse walls is becoming thick and cutinize. The dense parenchyma lying below the secretory epidermis undoubtedly contributes in the production of the nectar. The secretory tissues are supplied by vigorous marginal veins.

As shown in the pictures on Plate II all the epidermal cells have a big nucleus in the bottom of the cell. The outer wall in young parts has a great number of beaked papillae and shows also several cases of outbulging of the cuticle. Some delicate channels seem to reach the surface on top of the papillae. No pores were observed here but in a few cases a pore was detected outside a transverse wall separating two sister palisade cells which clearly had arisen by division of the same mother cell. In the young parts the transverse walls are not very thick, but in parts where the production of nectar may have taken place for some time, the outer parts of the transverse walls are thick and cutinized except in a very narrow zone of the most recently developed wall just outside the protoplast. This zone shows birefringence and is probably consisting mainly of cellulose. The thick parts of the transverse walls continue in thick outer walls in which the beaked papillae are much larger. The wall is traversed by many micro-channels. Obviously, at least two such channels, one from each side, proceed almost to the tips of the papillae. In a few cases a channel was traced from a papilla and into the middle part of a transverse wall. Some small cavities between wall layers outside transverse walls were considered to be part of the system of channels. It is assumed that the nectar flows through the fine channels and is liberated from the tips of the papillae. These may be formed by successive production of cuticular layers which in periods during which nectar oozes out may rupture and subsequently regenerate. The channels may, therefore, also be pathways for precursors of cutin. The beaked papillae greatly resemble similar structures observed by HABERLANDT (1904) in the outer walls of certain unicellular glands (by HABERLANDT estimated as hydathodes). EM studies of nectaria have been undertaken by SCHNEPF (e.g. 1964, 1965) and LEDBETTER & PORTER (1970, Plate 7, 4), who studied nectary cells in *Euphorbia milii*. These cells resemble those found in *Stillingia* by the position of the nuclei in the basal portion of the cells and by the thick cuticular layer which covers the top of the cells. LEDBETTER & PORTER also found intercellular spaces in the transverse walls near the top of the cells and add that such spaces conceivably channel to the free surface the sugar diffusing from the cells and from underlying vascular elements. The spaces found by LEDBETTER & PORTER are most probably comparable to the system of channels and cavities observed by us in the light microscope.

Outline of stem anatomy

The stem has eight concentric tissue layers surrounding a central pith, viz. epidermis, hypodermis, photosynthetic cortex tissue, parenchyma with numerous non-articulated laticifers, a thick layer of fibers, phloem, cambium, and xylem. In *Stillingia sylvatica*, HOLM (1911) describes six cell layers of collenchyma in the outer cortex and no hypodermis. *S. sylvatica* is a foliiferous, mesophytic shrub ranging from Virginia to Florida and westwards to Kansas and Texas. Its stem anatomy is very

different from that of *S. patagonica*, although both species are without endodermis in the stems.

Together with the epidermis the hypodermis very easily loosens from the photosynthetic cortex beneath. The cells in the latter form very regular radial rows and are clearly getting smaller abaxially (Fig. 3a). In some parts of the material the most peripheral green cells have recently been divided by periclinal walls. The peripheral cells are here short and placed on top of one another, as if they were formed by cambial activity. A few cells are divided by anticlinal walls and produce new radial rows. This dilatation growth appears to be independent of the increase in girth of the epidermis and hypodermis.

The fiber cells in this species are very large with a concentric lamellation which is particularly distinct (cp. Fig. 5a). Between the most distinct layers a number of very thin layers can be detected. The cell lumen in mature cells is very narrow and in longitudinal sections also very short or even absent over long stretches. A distinct layering in the fiber cell walls is also noticed by Holm (1911) for *S. sylvatica*.

In most of the cells four main layers can be distinguished, while in *Taxus* and other conifers there are only three (S_1–S_2–S_3), cp. Ledbetter & Porter (1970, Plate 6, 1). In *Taxus* these layers are separated by distinct lines and the cellulose filament orientation changes from layer to layer. In *Stillingia* the filament orientation is unknown, but separating lines appear mostly to be double (Fig. 5a, arrow), which may be due to the existence of a very narrow layer inserted between two broader ones.

Together with the xylem the cylindric layer of fiber cells constitute the main supporting system in *Stillingia*. There are no fiber strands in the peripheral cortex of soft photosynthetic cells. However, these tissues are protected by an epidermis which owing to its unusual structure must have mechanical properties.

The perivascular fiber layer is not continuous. Together with some large laticifers, groups of parenchyma cells interrupt the fiber layer. Such interruptions may occur in a few places in a cross section of a stem. They are probably necessary in order to make dilatation growth possible and as pathways for water and carbohydrates between the vascular tissues and the green cortex. It is not known in which way the very wide laticifers take part in the metabolic processes. They are placed just inside the green cells, and they contain great amounts of starch.

The xylem of the first annual ring appears to be very uniform without wide vessels. The second ring, however, has in the beginning a continuous layer with relatively large vessels. The rays are uniseriate and consist of upright or quadrangular densely pitted cells. The pith parenchyma has very thin-walled and large cells, but it hardly serves as a typical water storage tissue.

In the apical meristems the laticifers were traced to the sixth cell layer from the shoot apex. The laticifers contain many nuclei, sometimes with very large nucleoli. When using Johansen's quadruple staining technique, the nucleoli stained red but the same was the case with some very delicate, elongate structures which might be interpreted as cylindrical giant ER-spaces.

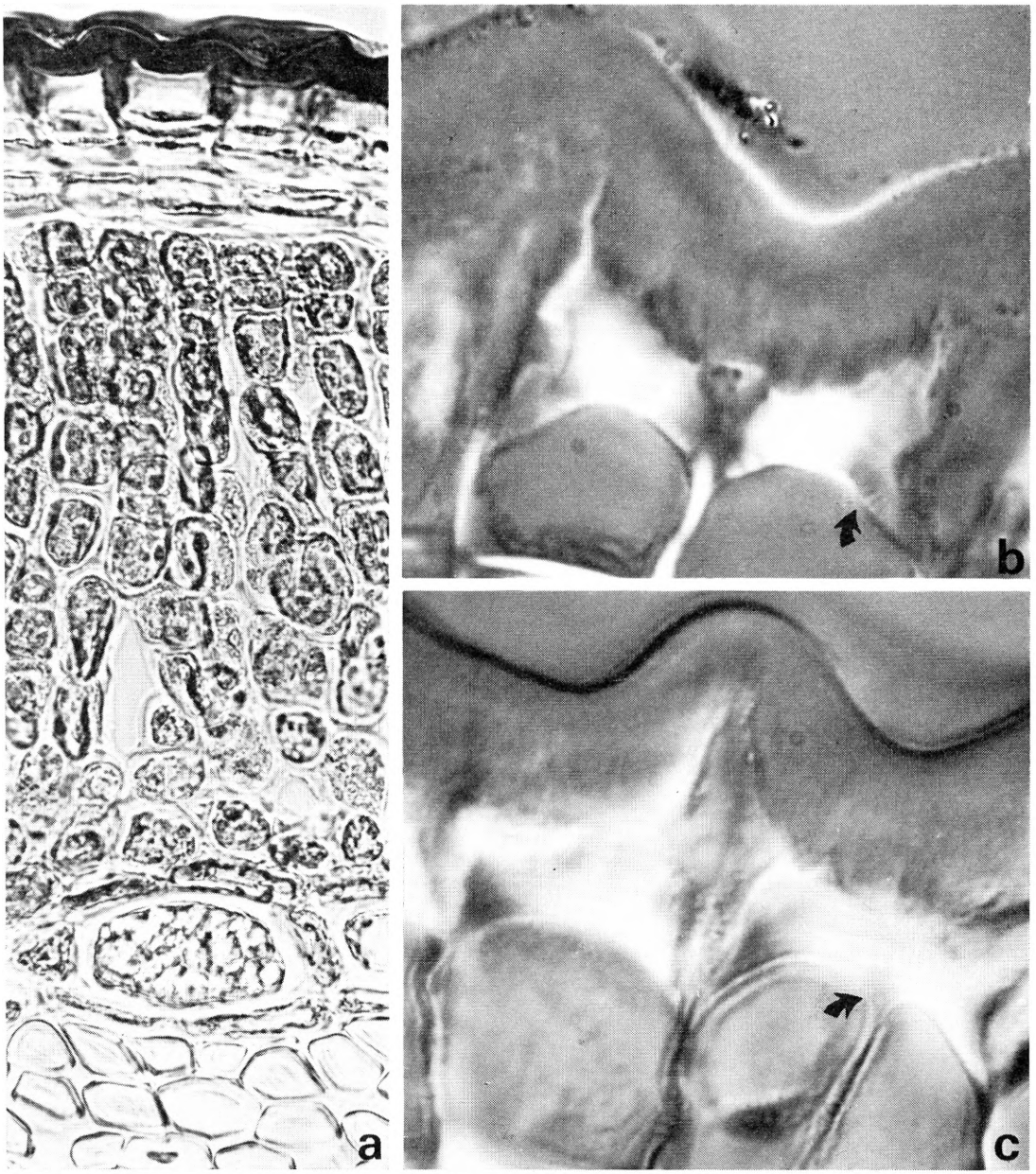


Fig. 3. *Stillingia patagonica*. a. Transverse section of stem. Sudan IV stains cuticular layer and flanges in epidermis. Below hypodermis many layers of chlorenchyma arranged in radiating rows. Inside chlorenchyma parenchyma with thick-walled laticifer and finally perivascular fibers (× 500). — b–c. Outer wall in epidermis stained with Sudan IV and observed in polarized light. Cuticular layer dark. Cellulose (and wax on surface in depression) showing up. In (b) radiating structures (possibly ectodesmata) at arrow. Tapering projections of cellulose inside bulges. Initial flange at arrow in (c) and broad flange under bulge traversed by very delicate lamellae (× 2000).

Epidermis

As observed in SEM pictures the outer surface of *Stillingia* appears densely foveolate (Plate I a–b). The foveae are deep, 5–10μ rarely 15μ, and elongate, 20–30μ long and 5–10μ broad. Most of them have a bottom which may be granulated (Plate I a–c), but many of the foveae also contain stomatal pores. These are difficult to detect when observed from above. The foveae which contain stomatal pores are particularly deep and become narrower upwards (Fig. 1c) and are frequently filled with ± loose scales or flakes which are birefringent and may be composed of some kind of wax.

Otherwise the surface is smooth and glabrous without trichomes or papillae, but the cuticle seems to break up into small flakes with an irregular ± dentate margin. (Plate I c–d). Some of the flakes appear to be more loose and roundish, about 10μ long, and are scattered regularly (Plate Ib) often being placed one in number near the margin of a fovea (e.g. on the right side of the stomatal opening in Plate Id).

The epidermis is usually one-layered, but may locally consist of two cell layers which cover a layer of tangentially elongate hypodermal cells.

Near the shoot apex the epidermal cells appear completely normal and there is no sign of foveae or localized thickening of the outer walls. Slightly below the meristem proper, however, the outer walls get covered by a cuticle and a thickening is started. At the same time the transverse walls in the epidermis appear irregular being provided with a single localized bulge. They are stretched in an abaxial direction and vacuolated in their outer part. The guard cell precursors are narrow and non-vacuolated. At an early stage hypodermis is clearly differentiated as a cell layer of axially stretched cells.

The walls of the outer epidermal cells are 15–20μ thick. When observed in polarized light the inner cellulose layer shows up brightly (Fig. 3b–c). The cuticular layer is about 10μ in thickness and continues in cuticular flanges placed outside the anticlinal walls. These flanges are large outside primary anticlinal walls, but small or initial where such walls are newly formed (Fig. 3c, arrow). The broad flanges are traversed by a system of very fine lamellae which may be cut up in fibrillae. These are mostly tangentially stretched strongly resembling similar structures found in *Verbena scoparia* (p. 89 and Plate XVIII) but not so distinct as in that species.

The cellulose part of the walls is lamellated but contains also a system of delicate, radiating striae or channels (Fig. 3b, arrow). The cellulose layer continues into a number of narrow tapering and branching projections into the cuticular layer. These projections are very large inside the bulges between the foveae. In most cases projections from two neighbouring cells run into the same bulge (Fig. 3c). In their distal parts the projections continue as branched micro-channels, but the many very delicate most distal branches are only visible when using interference contrast, and were difficult to photograph. They resembled the slender branched extensions of the fibrous cellulose layer into the cuticular layer described by Ledbetter & Porter (1970, Plate 7, 2).

In polarized light and when using the Red I plate, the cuticular layers show up

yellowish while the thick tangential cellulose layers turn blue. The projections are also yellowish, as are the anticlinal cellulose walls. The cuticular layer is deeply reddish coloured after treatment with Sudan IV, but the projections with their branches remain unstained. This shows that cellulose is present in the projections, and that the cuticular layer probably contains wax. The finest distal ramifications which continue the projections may be compared with ectodesmata, probably being pathways for wax- and cutin-precursors.

As already mentioned the strongest projections run into the bulges and may be formed at the same time as the cuticular wedges develop in connection with the anticlinal walls. In Fig. 3c the cell to the right is newly divided and a flange is initiated (arrow). It seems probable that the cutin formation in the flanges will continue and reach and merge with the outer cuticular layer. At the same time the activity near the small projections from the cellulose layer may increase resulting in a new bulge. The development of the cuticular flanges and the areas in the cuticular layer above was followed by comparing material taken at varying distances from the shoot apex. In relatively young parts the transverse walls seem to continue into the cuticular layer. From the plane which thus wedges into this layer a number of projecting, tangential layers are observed. The layers are relatively thick near the plane and become shorter with increasing distance from the living part of the cell. Observations in polarized light make it very probable that the lamellation near the plane is due to the deposition alternately of cellulose and cutinized layers (Fig. 4c). As already mentioned this lamellation can be followed also in older parts where, however, the plane is widened to a wedge-shaped area tapering towards the outer surface. This widening appears to take place simultaneously with that which happens in the flanges where the wedges, however, taper in the opposite direction. The whole process clearly leads to an increase in girth. In this connection the complete absence of fissures or ruptures in the cuticular layer should be discussed. The surface is intact, and this fact may be explained by assuming a growth, parallel with the surface, of the cuticular layer particularly in the areas of the bulges and flanges. During this growth we may imagine that cutin is formed and deposited, but also perhaps that cutin somewhere may be decomposed and regenerate.

The flanges have a very irregular surface towards the cellulose parts of the walls. Also the tangential inner surfaces of the cuticular layer are more or less rugged. In a few cases roundish small cutin areas were observed close to but apparently separated from the continuous cuticular layer. Such small "cutin balls" have almost the same size as the small convex protrusions in the rugged cuticular surface and are possibly connected with these by cutinization of the intermediate cellulose space. The "cutin balls" may be comparable to the so-called cutin-cystoliths mentioned by Martin & Juniper (1970, Fig. 4. 1).

The stomatal apparatus appears from Fig. 1b–c, 4 a–b, and Plate Id. The guard cells have very thick outer and inner walls. The front cavities are bordered by thick cutinized walls (Fig. 4 a–b). The cavity is 10μ high, almost cylindrical, and abaxially

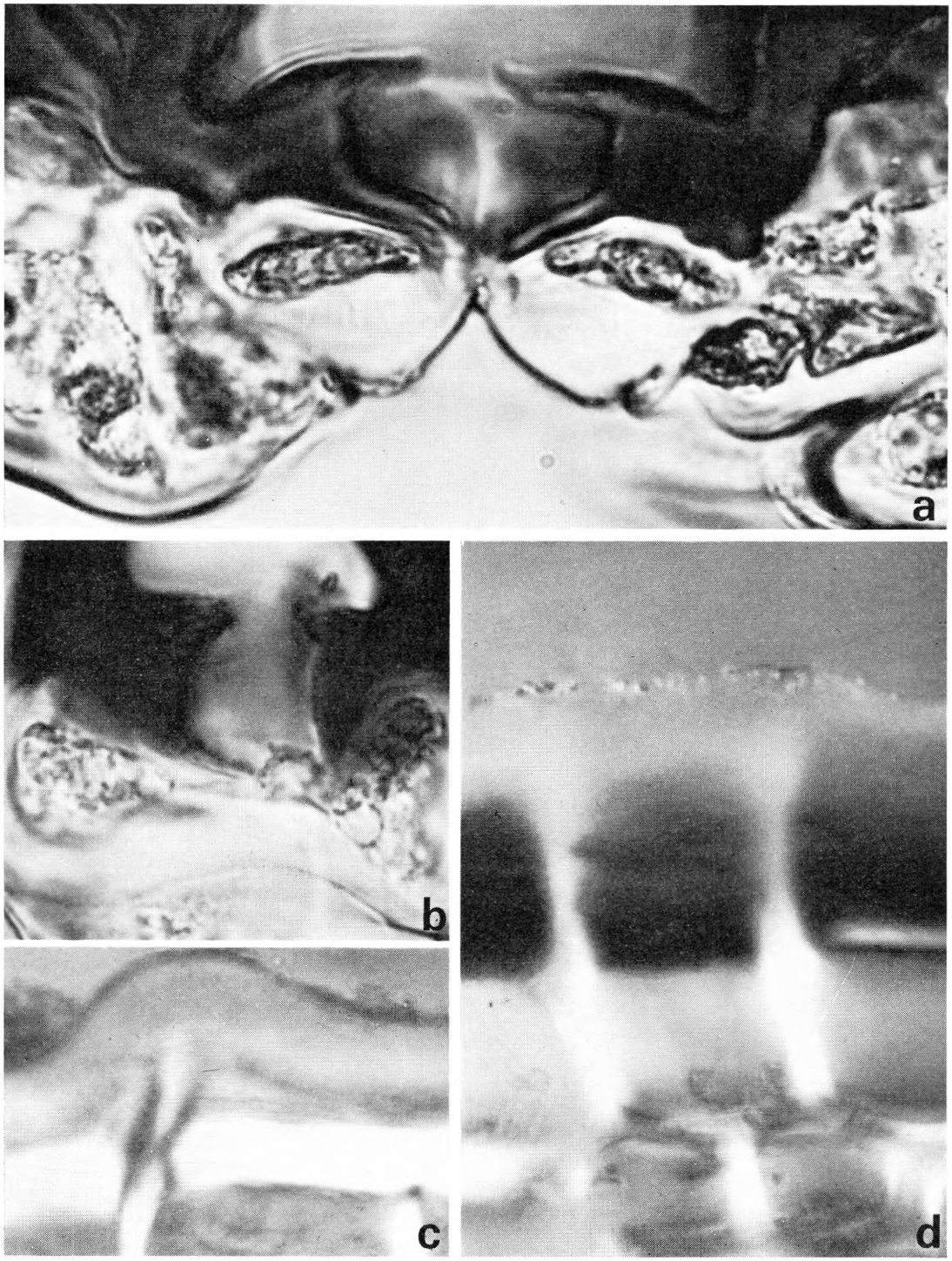


Fig. 4. *Stillingia patagonica*. a–b. Stomatal opening in cross section (a) and longisection (b) stained with Sudan IV showing complete cutinization of front cavity. In (a) radial striae in thick inner cellulose walls of guard cells. — c–d. Development of bulges and flanges in outer epidermal wall, in rather young (c) and mature wall (d). c. In polarized light and stained with Sudan IV showing subsequent deposition of lamellae of cellulose (light) and cutinized lamellae (dark). Cuticular flange developing in continuation of primary transverse wall, no such flange yet above newly formed wall on the right. Light areas in outer part probably due to wax contents. — d. In polarized light and with the Red I plate. Transverse walls continuing into cuticular layer. Bright shining parts of transverse walls indicating cellulose, faint shining parts in outer part of wall as well as small shining grains on surface probably due to wax (× 2000).

it is greatly narrowed at the front ledge, which forms a diaphragm (Fig. 1 b) resembling that observed in *Bredemeyera colletioides* (Part I, Plate XVI a–c). The inner walls of the guard cells are not cutinized but consist of cellulose lamellae which are proximally traversed by some delicate radiating striae (Fig. 4 a). The thinner walls towards the subsidiary cells are very short appearing as thin-walled corners between the outer and the inner walls. It is difficult to imagine how the stomatal movements take place. The guard cells, however, have relatively thin-walled bulbous ends which may swell almost as in grass-stomata. In this character they resemble the stomata described by Fahn (1967: 148) in *Haloxylon articulatum*.

In the case of *Stillingia* stomatal transpiration may be reduced by the existence of double front cavities, as the cavities formed by the guard cells are found at the bottom of deep foveae in the epidermis (cp. further p. 126).

The Cassia aphylla group

Cassia aphylla Cav. (*Caesalpiniaceae*) is a member of a natural group of taxa which has been evaluated as separate species or as varieties of *C. aphylla*. The group was treated anatomically by Schwabe (1950), who separated six taxa all without trichomes. Schwabe referred the taxa to *C. crassiramea* Benth. and *C. aphylla* Cav. with the varieties *divaricata*, *trichosepala*, *robusta*, and *rigida*. The material available to us belongs to *C. crassiramea* and to three of the *C. aphylla*-varieties of which now one, *C. rigida* (Hieron.) Burkart, has been raised to specific level. Within *C. aphylla* we have studied var. *aphylla* and var. *divaricata* Hieron.

Schwabe tried to utilize the presence of dark reddish-brown pigments in the hypodermis and the parenchyma cells in the interior of the stems in order to distinguish the taxa anatomically, but she admits (1950, p. 177) that the pigmentation may be influenced by climatic conditions. Our observations confirm that the pigmentation is not a reliable character. Thus, the material of *C. rigida* which was determined by professor A. Burkart has a high degree of pigmentation, while in the key given by Schwabe *C. rigida* is said to be without pigmentation. Under these circumstances we have chosen to treat the material from the various taxa together in spite of the possible existence of a number of smaller constant anatomical differences between them.

Material

C. aphylla var. *aphylla*. Monte-vegetation 39 km south of Mendoza, Prov. Mendoza, W. Argentina. Böcher, Hjerting & Rahn No. 2094, Jan. 5, 1956. Seeds were also collected from this locality and plants raised which are now in culture and have been included in the investigations.

C. aphylla var. *divaricata*. Specimens from Prov. San Juan, W. Argentina 1000 m. above sea level. 267 km from Mendoza. Böcher, Hjerting & Rahn No. 2253, Jan. 10, 1956.

Fig. 5. *Stillingia patagonica*. Fiber cells in transverse and longitudinal sections showing lamellation. In the upper picture on the left thick-walled laticifer and parenchyma accompanying laticifer. (Interference contrast, × 2000).

C. rigida. Prov. Salta, NW. Argentina, Dept. S. Carlos, San Lucas, 2100 m. above sea level. Dry Monte scrub. Hawkes, Hjerting & Rahn No. 3516, Febr. 16, 1966.

C. crassiramea. Prov. Jujuy, NW. Argentina, Dept. Tilcara, Gargante del Diablo, 2950 m. above sea level. Hawkes, Hjerting & Rahn No. 3792, Mar. 10, 1966.

Occurrence and morphology

C. aphylla and allied species are typical representatives of the subtropical bush steppe vegetation which in Argentina is called Monte. Examples of habitats are described in Böcher, Hjerting & Rahn 1972. Typical *C. aphylla* is a very much branched low shrub, sometimes almost a dwarf shrub. The sympodial system of delicate green shoots is often arranged in zigzag, but pseudo-dichotomous branching also occurs. Small dark scale leaves support new branches which—where they issue from their mother shoot—are surrounded by short white trichomes. Otherwise the surface is glabrous but may locally be covered by small flakes of waxy material. Resinous substances are observed in connection with some of the axillary buds. *C. rigida* is taller, up to 3 m., with coarser and more rigid branches.

Outline of stem anatomy

Schwabe (1950) gives a number of figures showing very schematically the main outlines of the anatomy. These figures also inform about the variation in pigmentation and contents of crystal druses.

In the stems eleven different layers can be distinguished. They appear from our Fig. 6 and Plate III a.

(1) Epidermis
(2) Hypodermis
(3) Outer photosynthetic cortex of palisade cells.
(4) Inner cortex, resembling (3) but the cells shorter and frequently containing many crystal druses.
(5) Layer with many sclereids and crystal cells. On the abaxial side of the fiber strands (6) the layer only contains crystal cells. Presumably it represents the endodermis.
(6) Strong fiber strands placed outside the protophloem and therefore probably phloem fibers.
(7) Layer of large parenchymatous cells, which in many cases seem to degenerate or to be dissolved.
(8) Phloem
(9) Cambium
(10) Xylem; axial parenchyma often vasicentric.
(11) Pith parenchyma. Some of the cells with brownish contents (Plate III a).

A comparison with the stem of *Cassia kurtzii* Harms shows that this species has a similar stem structure, in which, however, the green cells do not form a palisade tissue and the endodermis has fewer crystals in the cells. *C. kurtzii* is a Patagonian

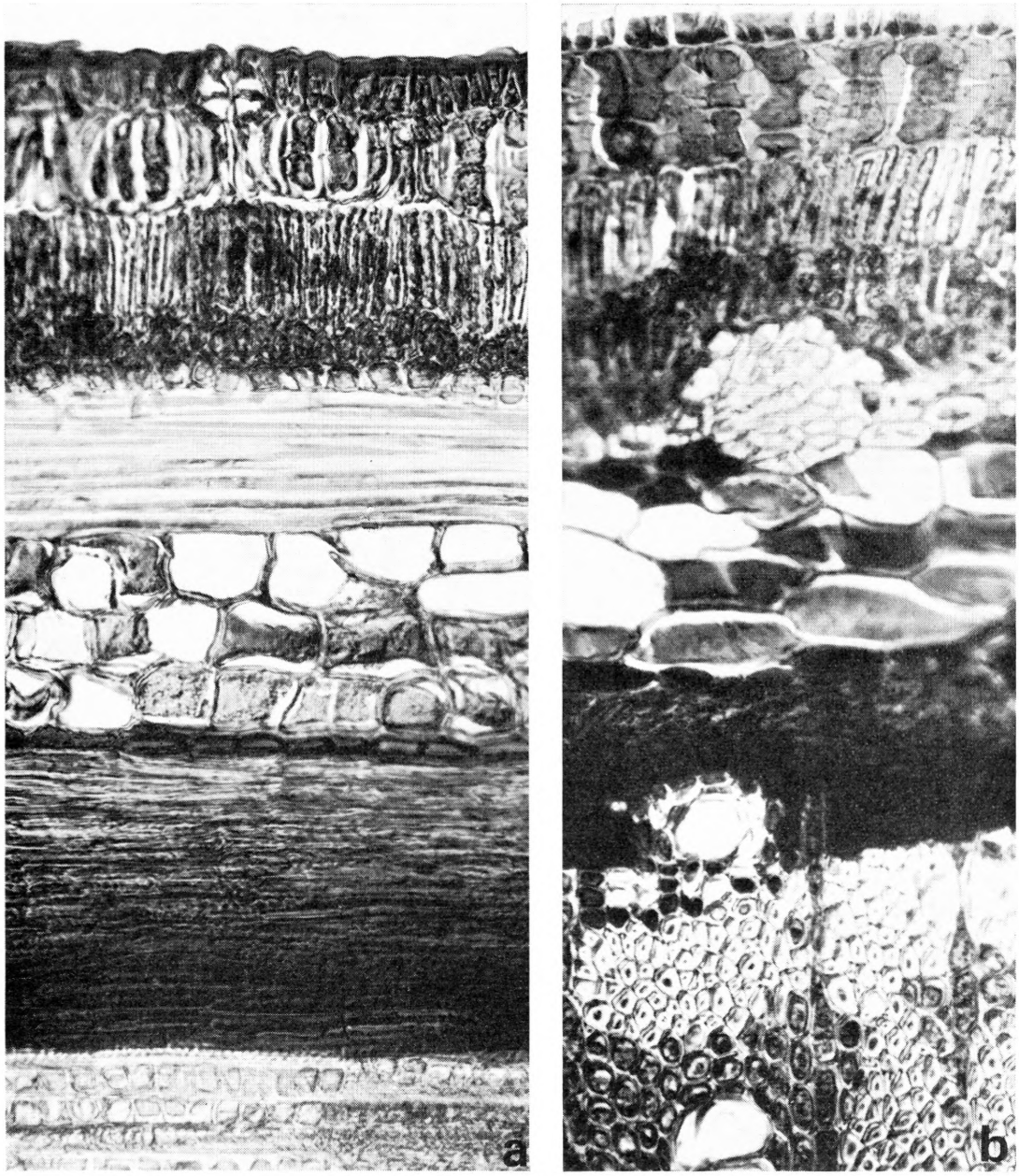


Fig. 6. *Cassia rigida.* a. Longisection of stem stained with Sudan IV, — b. Transverse section. Johansen's quadruple staining. Note difference in wall thickness in hypodermis in the two sections, in (a) stomatal opening and very narrow intercellular space in hypodermis below, layer with crystal cells (endodermis?) outside fiber strand. In (b) sclerenchymatous cells on both sides of fiber strand. Dark cell contents in hypodermis, cortex palisade, phloem parenchyma, cambium and xylem rays. In (a) elongate group of small thick-walled cells on the border between the large parenchyma cells and the phloem; prismatic crystals (together with numerous minute acicular crystals) closely packed in axial xylem parenchyma. In (b) band of xylem fibers and young fibers and wide young vessel surrounded by dark cells in cambial region (× 320).

dwarf shrub and not a true apophyllous plant. It bears small trifoliate leaves which largely are shed during the winter. The cuticular layer on the green branches in this species is not very thick and there are hardly any cuticular flanges as in *C. aphylla*. The fact that the stomata are not sunken contributes to the impression that *C. kurtzii* is less xeromorphic. This impression also agrees with its type of occurrence in the foothills of the Andes (see BÖCHER, HJERTING & RAHN 1972 pp. 256-259).

Epidermis

The surface in *C. aphylla* aggr. is smooth or appears granulated. Observations in polarized light of transverse sections reveal the occurrence of wax, either as irregularly granulated deposits or as rods. These wax layers are placed outside the cuticular layer and the cuticle (Plate V e–f). They are often removed by the alcohol treatment. Inside such wax deposits the cuticular layer is traversed by many delicate strands or micro-channels (highly resembling ectodesmata) which stop beneath the cuticle (Plate V d). The wax deposits become flaky and sometimes loosen thus making the surface granulated (Plate IV a). The system of micro-channels appeared to be very dense, and in one part of the material (*C. crassiramea*) it was possible on tangential sections of the stem by using interference contrast to establish a branching of the strands in the outermost part of the cuticular layer (Plate V d).

The stomatal openings are always orientated at right angles to the axis of the stem. In SEM micrographs (Plate IV a, c) they appear as narrow stripes bordered by two almost parallel lips. The pore is about 5μ wide and 25–40μ long. In *C. crassiramea* the pores are slightly deviating. The guard cells in this species only sink slightly below the surface but are covered by the protruding subsidiary cells which, therefore, become visible on SEM pictures (Fig. 10 d) by framing the opening on two sides.

The outer epidermis walls increase in thickness, and the cuticular wedges between the cells grow deeper and wider. From the beginning the subsidiary cells are narrow, but in older twigs they elongate very much and their abaxial part tapers into a single narrow strand. This growth of the subsidiary cells brings about an overarching of the guard cells and the formation of the narrow outer front cavities observed from above on the SEM micrographs and in transections in the light microscope (see Plate IV).

Fig. 7 a and 11 a (arrow) show the first sign of stomatal differentiation. By a cell division two very narrow cells are formed which have elongate nuclei and very dark cytoplasma with only few and small vacuoles. In almost all cases the fixation (FAA) brings about a withdrawal of the cytoplasma from the walls separating these cells from their neighbours. When comparing these pictures with those of young mature guard cells it appears that the guard cells during their growth must curve and push their back walls into the subsidiary cells which at the same time become crescent-shaped.

Young epidermis cells are quadrangular and have thin outer walls (Fig. 11 a), but already in the second and third internodium the outer walls begin to increase in thickness, and the first signs of cutinization appear.

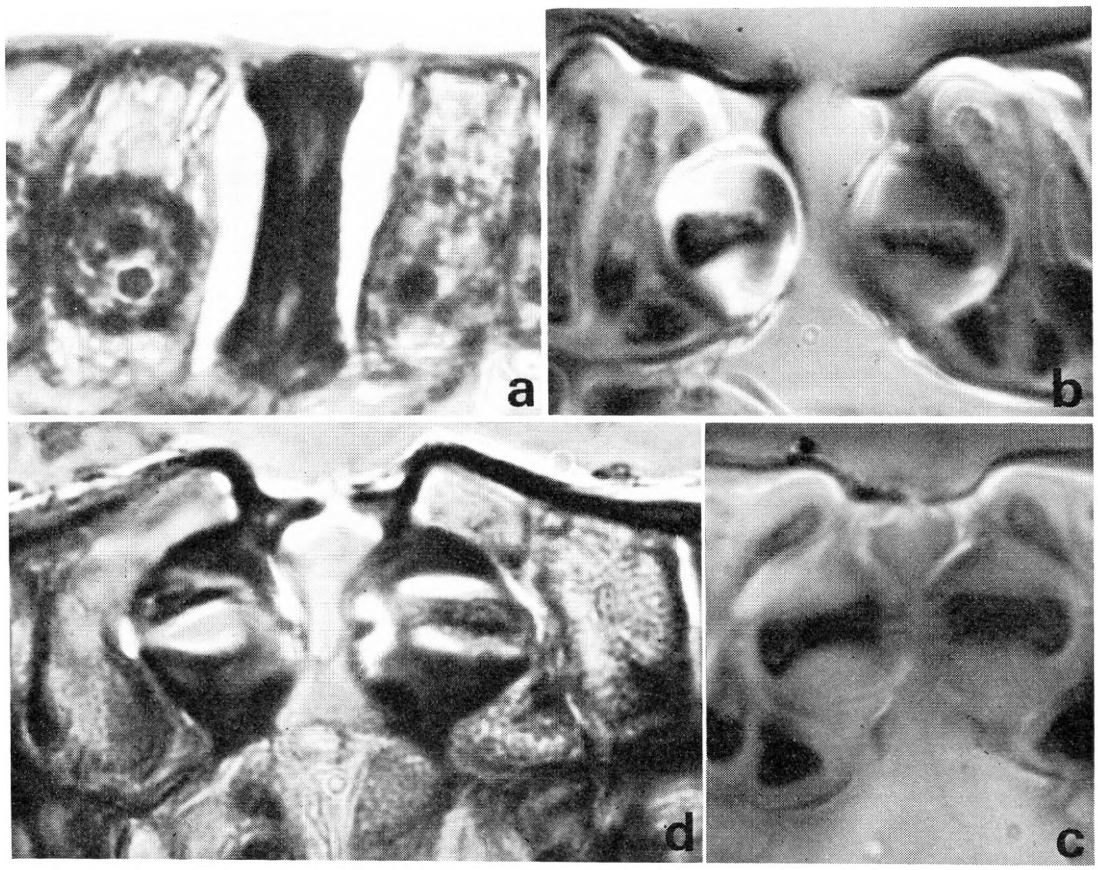


Fig. 7. *Cassia aphylla* aggr. — Longisections of stems showing development of stomatal apparatus. — a. Very young stage showing dark guard cell precursors heavily plasmolyzed on the sides towards the precursors of the subsidiary cells. — b–c. Young guard cells, in (c) structures resembling ectodesmata, issuing from guard cell protoplast and continuing towards pore (interference contrast). — d. As b–c but quadruple staining, thick parts of guard cell walls and interior outer wall layers of adjacent cells dark blue (due to contents of cellulose) (× 2000).

By increasing thickness and girth the epidermis cells divide and form small cell families which in paradermal sections appear as groups of two-four cells separated by relatively thin walls but surrounded by thicker walls towards neighbouring families (Plate IVb).

The guard cells are provided with outer ledges issuing from the thick outer walls and from the top of the subsidiary cells. Inside these ledges a small inner front cavity is formed, which is about 10μ wide and about 5μ deep. The front cavity continues inwards in a very narrow fissure formed by the middle parts of the guard cells which with increasing age elongate and become less curved (cp. Fig. 8 and Plate IVd). Having passed the proximal tapering living parts of the cells the fissure widens a little but narrows again at the low inner ledge issuing from the inner thick walls of the guard

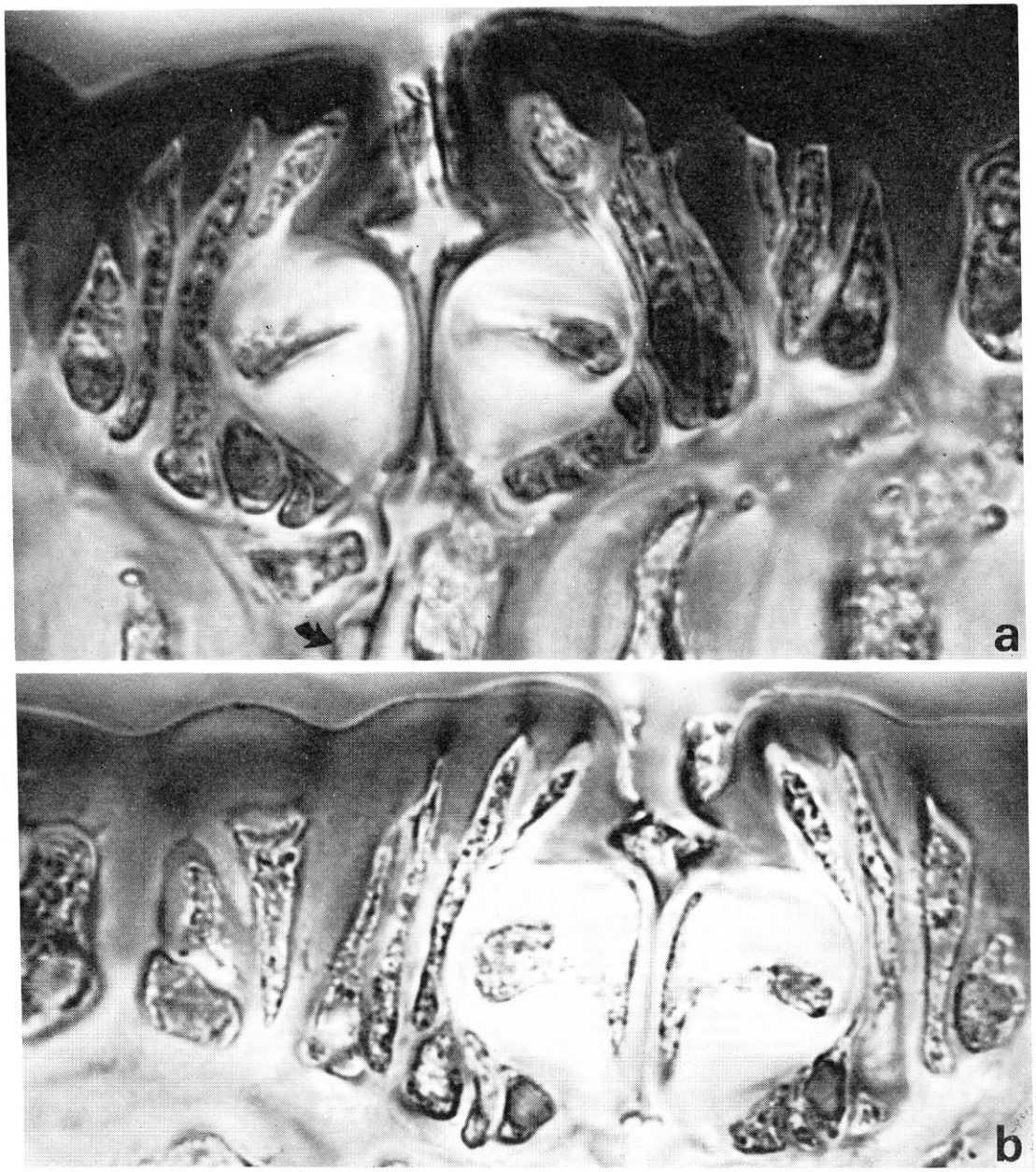


Fig. 8. *Cassia aphylla* aggr. a–b. Longisection of stem stained with Sudan IV showing guard cells, many subsidiary cells overarching guard cells and forming sheltered area outside front cavities. In (a) the outer part of the hypodermis and the very narrow substomatal cavity are seen. The latter has cutinized walls (arrow). In (a) the guard cell protoplasts are shown in the central position while in (b) they are closer to one of the ends of the cells, while the proximal parts form narrow extensions along the pore, cp. Fig. 10 (× 2000).

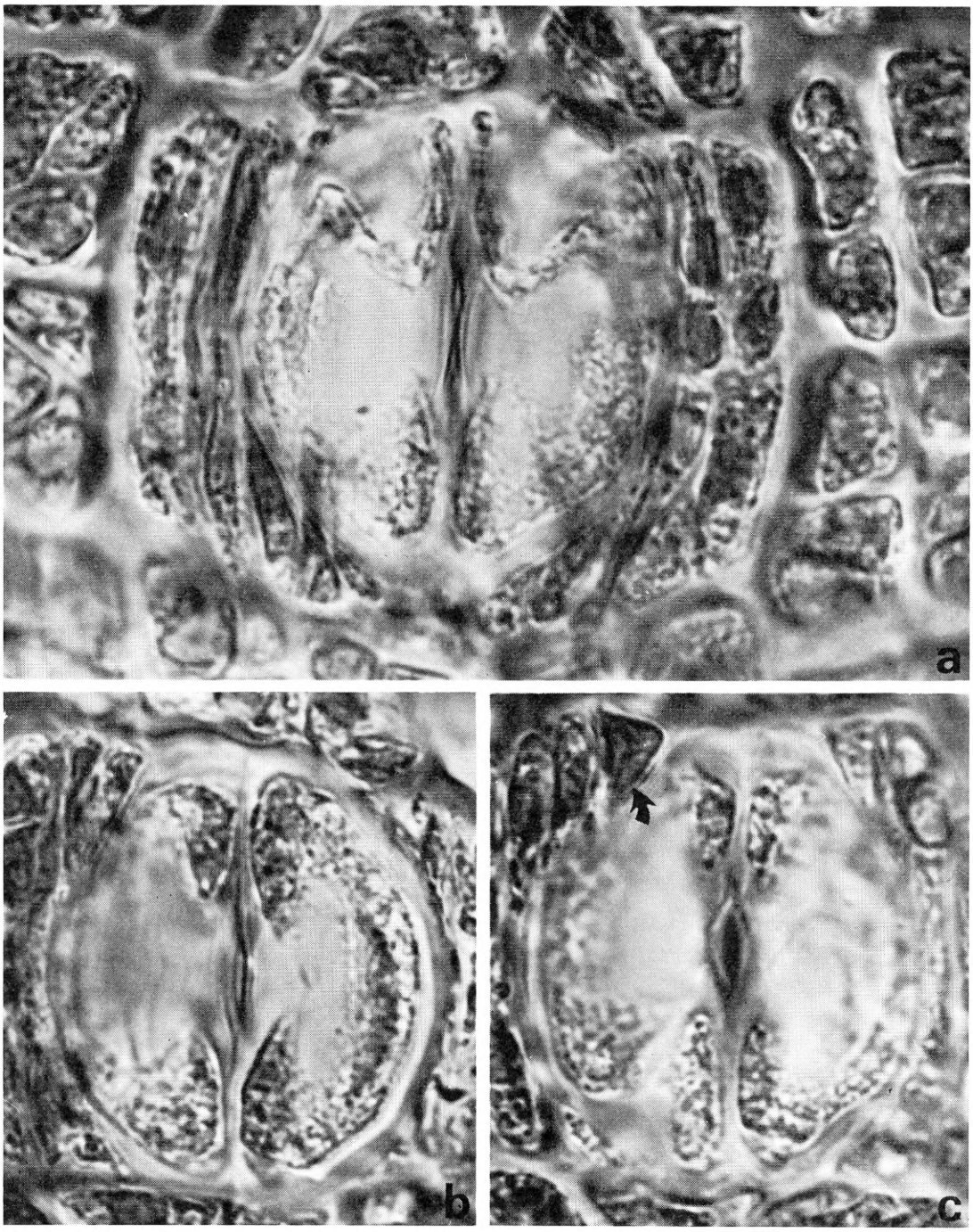


Fig. 9. *Cassia aphylla* aggr. — Surface view of stomata. — a. At high focusing showing thickened cell wall at one end (upper) and very thick wall off central pore. The guard cells surrounded by numerous subsidiary cells. The normal epidermis cells divided forming groups of cells with the same mother cell. — b. At deeper focusing showing narrow central pore and guard cell protoplasts having the shape of telephone handsets; very thin protoplasmic plate connecting the two terminal parts. — c. Still deeper focusing, inner ledge surrounding central pore; flat peripheral parts of protoplast ending abruptly (cp. Fig. 8 b), at arrow the bulbous inner parts of one subsidiary cell (×2000).

cells (Fig. 8a). In the young stage the guard cells measure 10μ in breadth off the central pore and the living cell lumen; older cells have increased their breadth with about 3–5μ. This increase is mainly due to a thickening of the proximal walls facing the fissure. At the early stage delicate micro-channels or ectodesmata are observed between the fissure and the living part (Fig. 7c), a position which corresponds to the ectodesmata which in *Zantedeschia aethiopica* occur closest to the central pore (FRANKE 1967, Fig. 6). Structures of this kind could not be detected in older guard cells, a fact which makes it probable that the channels serve as supply lines during the cell wall growth. They may be responsible for a peristomatal transpiration which perhaps here takes place mainly in young parts.

The subsidiary cells increase in number and elongate very much, their middle parts become very narrow and at the same time they taper outwards and swell inwards towards the hypodermis (Fig. 8). In surface views (Fig. 9) the guard cells are surrounded by numerous cells which are either subsidiary cells or derived from such cells. The guard cell protoplasts, although slightly plasmolyzed, have a striking appearance. Outside the central pore they resemble two symmetrically arranged telephone handsets. The thick distal part of the cells forms two semicircles along the walls towards the subsidiary cells. Where the two guard cells meet, the protoplasts are also thick, but in the middle part of the central pore they are very thin and difficult to detect. However, in transections this thin part is quite clear (Fig. 10). On transections the distal part is seen as a narrow almost cylindrical plasmatic body containing the elongate nucleus in the middle (Fig. 10b).

Scale leaves; axillary emergences and trichomes

The scale leaves are very small. At an early stage the distal part of these scales is separated from the base by phellem which sooner or later will function as an abscission layer (Fig. 13a). The cells of the distal part get lignified walls and die. In a very early stage the scale is traversed by a vascular strand in which tracheids play an important part and continue right to the top of the scale. It is assumed that scale leaves at the very early stage act as hydathodes. From Fig. 13b showing the tip of a young scale leaf it appears that the tracheids approach the axial surface and run along some very large empty cells.

A few living cells are placed in continuation of the tracheids and may serve as a kind of epithem. However, some of the cells which are inserted between the tracheids and the empty cells are extraordinarily large and contain nuclei four times bigger than normal ones. They resemble nuclei in glands. Some of the cells are tracheoid (tracheid-like and short) and may have water-storing function ("Speichertracheiden").

The scale leaves support buds or branches. The axils also contain some emergences which resemble the branched glandular hairs found in *Mimosa* (see METCALFE & CHALK, Part I p. 478). In young parts (Fig. 11) these emergences are elongate bodies in which the uppermost cells are rather big and tend to grow out almost as fingers (Fig. 11a, c). These cells contain large nuclei and have cutinized outer walls. In many

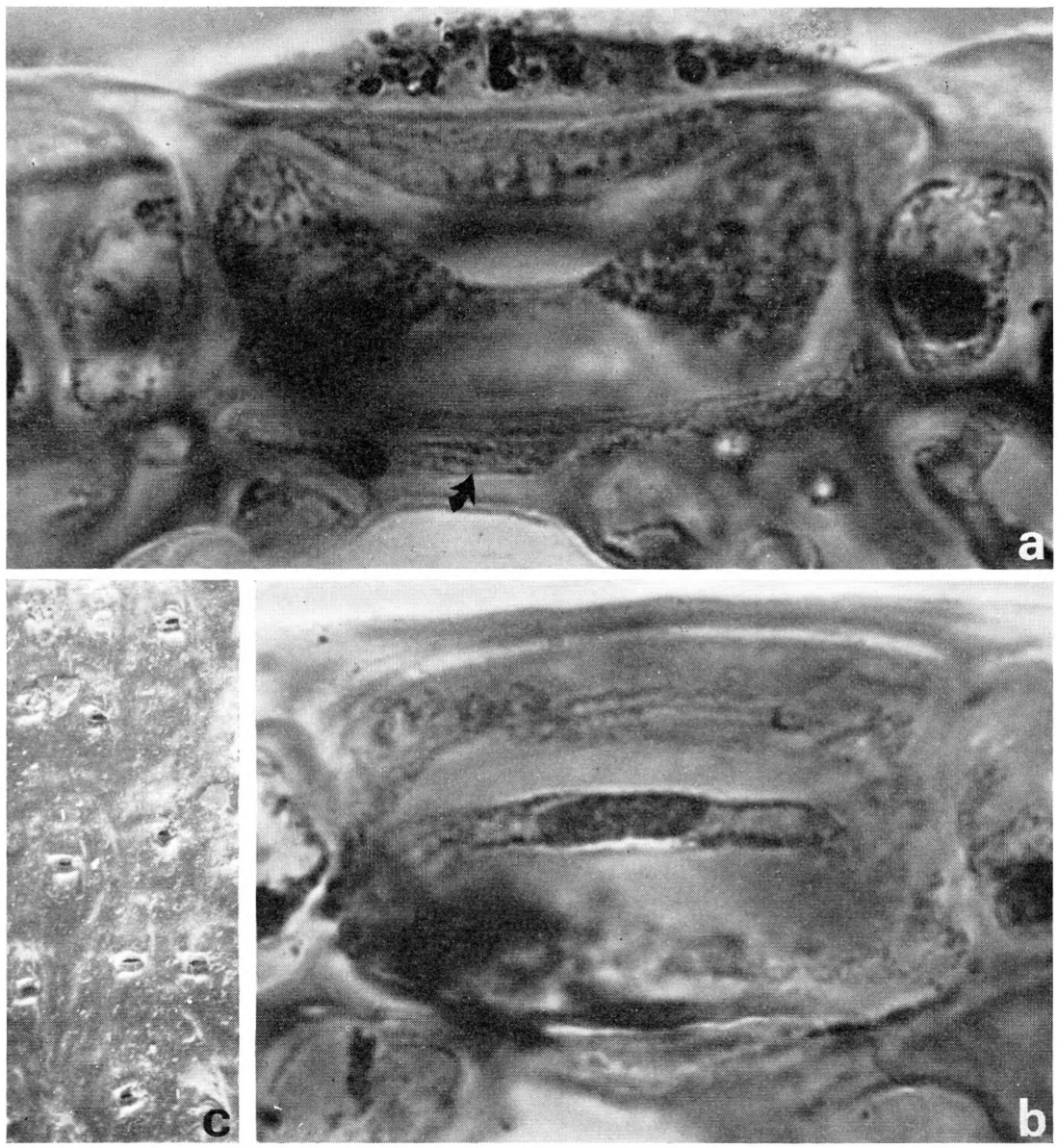


Fig. 10. *Cassia crassiramea*. a–b. Transverse sections of stem showing entire guard cell. — a. Facing central pore where the middle part of the protoplast is very thin while the ends are bulbous although flattened (cp. Fig. 8). Dark shade above thin middle part is the nucleus (cp. b). The elongated protoplast (at arrow) is the bulbous interior part of the subsidiary cell next to the guard cell. — b. Same guard cell as (a) but at deeper focusing showing backside of the cell with protoplast almost as a cylindrical body containing the nucleus (× 2000). — c. SEM micrograph showing position of stomata and smooth surface. Guard cells visible, not sunken, cp. a–b (× 205).

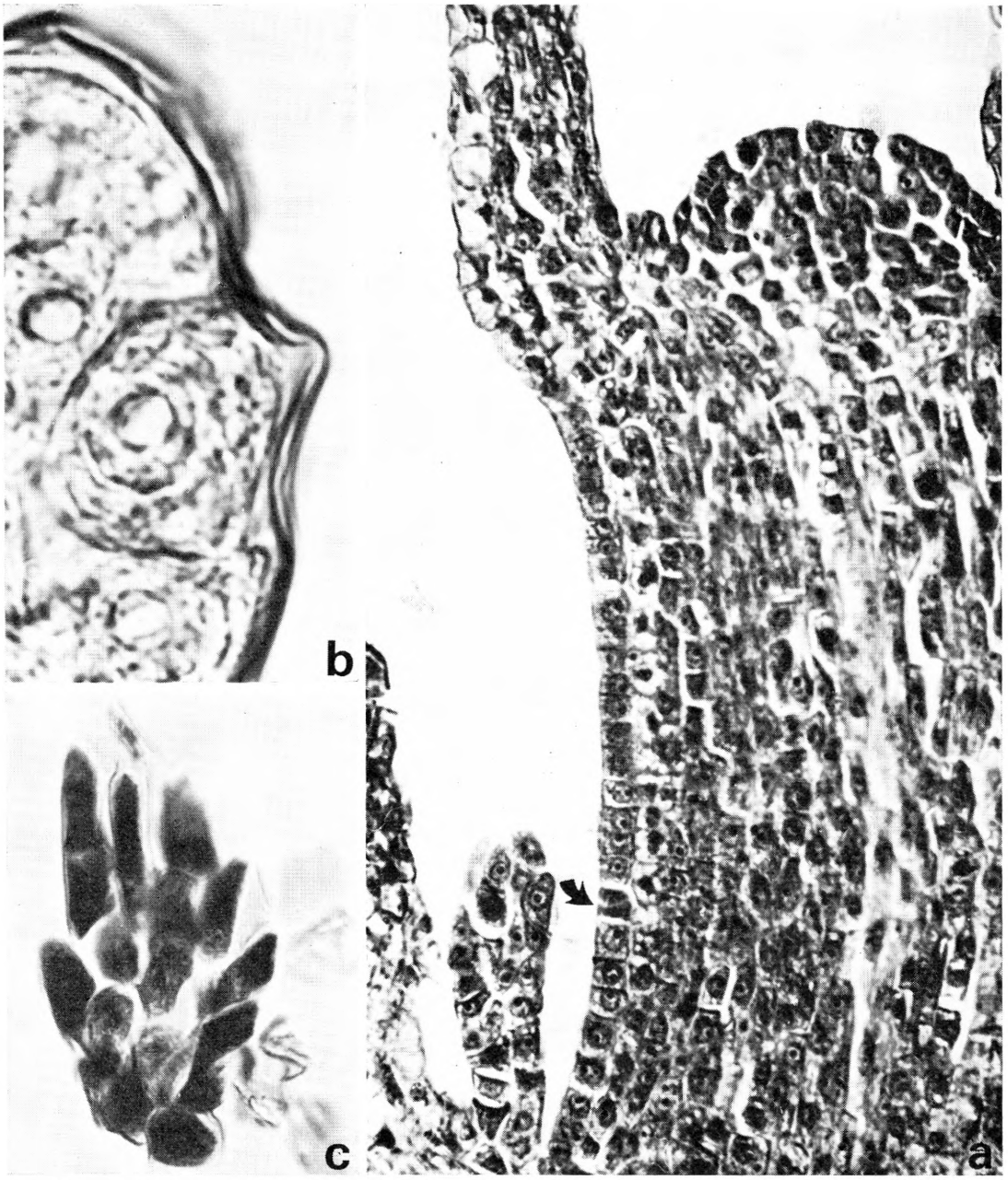


Fig. 11. a. Shoot apex of *Cassia aphylla* showing two nodes, in the uppermost axil emergence primordium, in the lower axil the emergence is well developed and has about five finger-like extensions (left side of arrow); arrow pointing towards guard cell precursors in epidermis. Hypodermis clearly differentiated from epidermis and cells developing into palisade tissue (× 410). — b. Top of emergence showing cuticle (Sudan IV staining) and beaked cell (× 2000). — c. Emergence with about eight finger-like extensions (× 500).

cases they carry a short beaked excrescence in which the tip has a very thin wall (Fig. 11b). Some of the longitudinal walls also seem to be cutinized. In this young stage these emergences seem to function as glands. Later they undergo considerable changes. In the basal part the cells become empty and get suberized walls, thereby resembling the scale leaves with their abscission cork layer (Fig. 12a). In the upper part the large cells degenerate and fuse. An early indication of degeneration may be a large contents in the cytoplasm of substances which stain with Safranin. Later the cell walls are dissolved and become mucilaginous. Some of the emergences are less well defined and seem not to have basal suberized cells. They occur in the ring-shaped furrows at the base of branches together with uni- or bicellular trichomes which are air-filled, non-living and have cutinized walls. Such trichomes issue from the bottom of the furrow. Other trichomes are not cutinized and seem to cover additional suppressed and dormant, perhaps seriate buds in the axil.

Beneath the furrows a tissue of small living cells is formed (Fig. 12b). The small cells often divide and the tissue contributes undoubtedly to the dilatation growth of the cortex. Below the small-celled tissue and the furrow short tracheal cells occupy a big fan-shaped area (Fig. 12b) radiating from the xylem. It is possible that water or slime under certain conditions are released through the living cells of the emergences, but an absorption of water which drains down in the furrow may likewise be considered possible. Some of the hairs here are not cutinized, and the small cells below such hairs are living.

Hypodermis

As pointed out by H. Schwabe (1950) the hypodermis in the leafless *Cassia* species has very thick walls. The walls often contain a reddish-brown pigment. The thickness of the walls and the pigmentation vary also in our material.

In very young branches the hypodermis cells have thin walls and divide mainly by anticlinal walls. Fairly soon, however, also periclinal walls are formed (Fig. 13a) and the walls begin to thicken. At this stage they are intensely stained by Fastgreen. Later the thickness increases very much and it is obvious that the radial axial walls are much thicker than the horizontal transverse ones (Fig. 6).

The larger increase in thickness of the radial walls is clearly of importance for the dilatation growth of the cortex. The thick walls do not show any sign of lignification but get yellowish or brownish. The thick walls are always primary ones, while new periclinal walls stay rather thin (Plate VIb). The secondary walls are traversed by numerous long pit canals. By using interference contrast very delicate plasmodesmata can be detected between the opposite pits. Using the same optical equipment the pit canals appear lined (Plate VIc). The mature hypodermis in the *Cassia aphylla*-aggregate has a striking resemblance to the hypodermis described by Nommensen (1910) in *Echinocactus lecontei*. In this species the hypodermis shows similar thickness of its walls and long pit canals. Chemically the thick walls were assumed to be composed of cellulose although it is stated that even after long treatment with iodine and

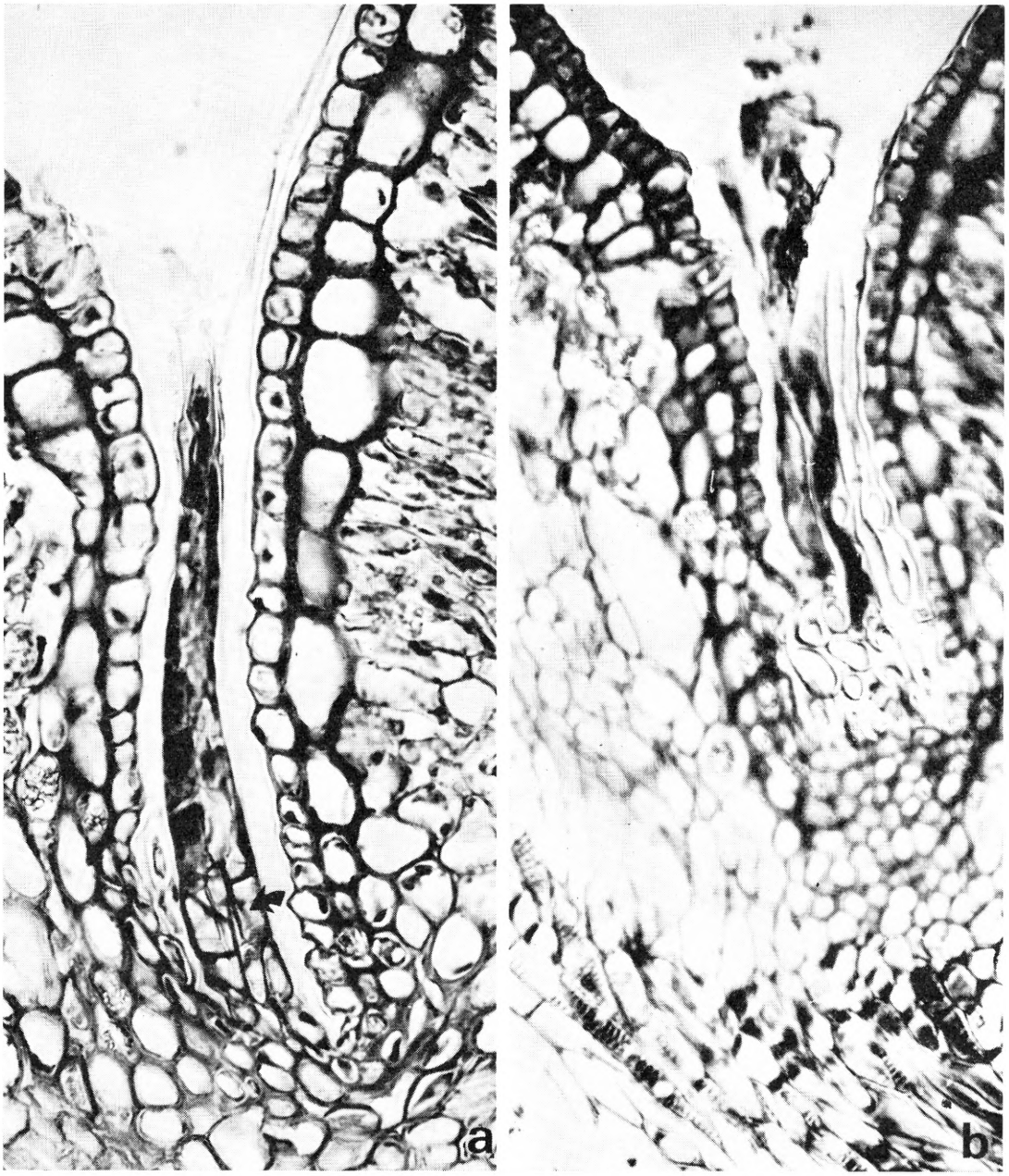


Fig. 12. *Cassia aphylla*. Young upper part of plant. Ligule-like emergences in furrow at the base of branch (on the left), quadruple staining. — a. The upper cells are mucilaginous, at arrow the cells have suberized walls (abscission layer), the basal cells are living; note large hypodermal cells (× 500). — b. Later stage showing decomposition of upper part of ligule-like emergence and the occurrence of hairs in the bottom of the furrow. Below furrow tissue of small cells which downwards are connected with tracheoid cells occupying fan-shaped area (× 320).

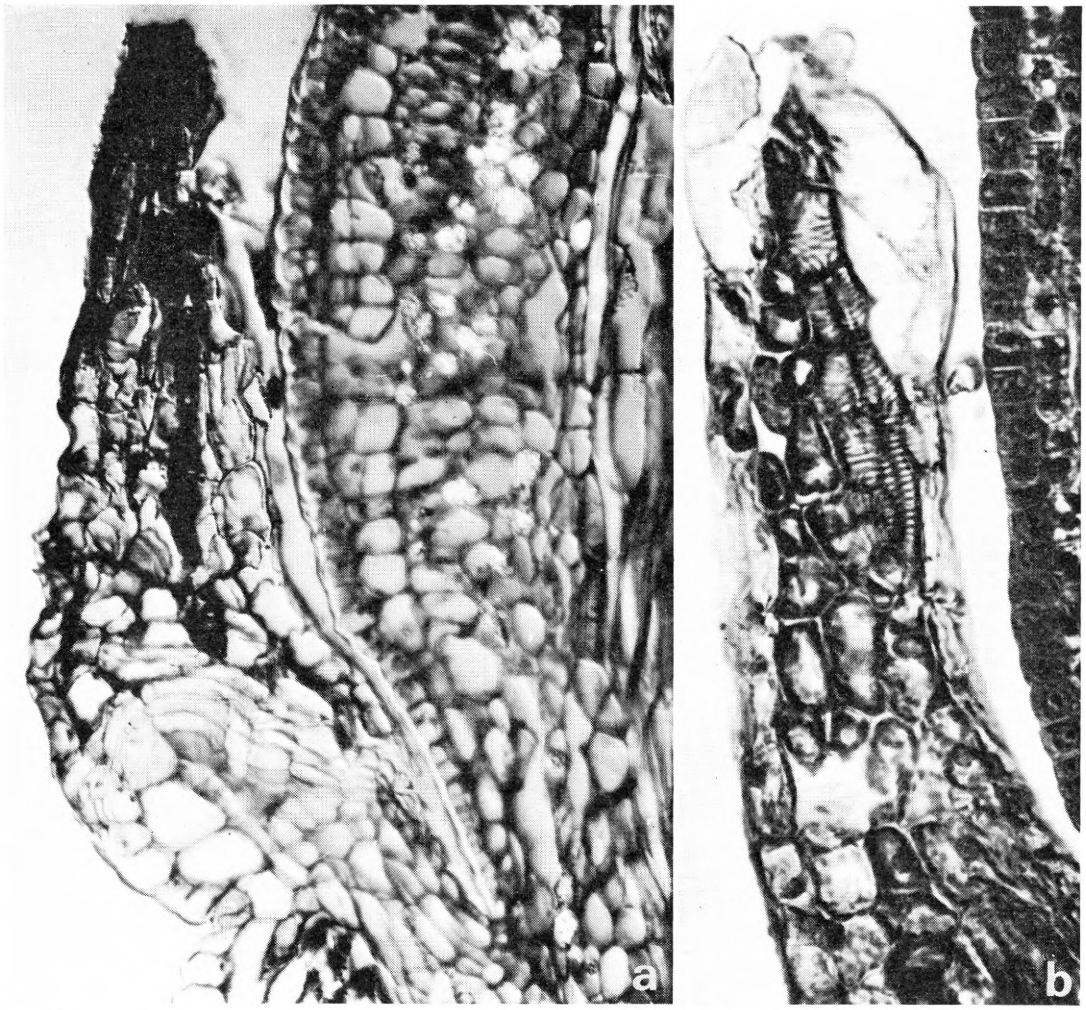


Fig. 13. *Cassia aphylla.* Longisections of scale leaves. — a. Abscission cork layer distinct at base of scale, in stem, division of hypoderm cells, crystal druses in cortex cells showing up, as are single row of fibers on the right. — b. Tip of scale leaf; numerous tracheoid cells surrounded by large empty cells forming the tip which at this stage may function as a hydathode and perhaps in moist periods be able also to take up water (Interference contrast, quadruple staining, × 320).

zinc chloride the walls attained only a weak bluish tone. The hypodermal cells in *Echinocactus* deviate from those in *Cassia* by their regular contents of cilicous bodies and by the fact that the cells seem to die. According to NOMMENSEN similar hypodermal layers are found in the genera *Cereus, Echinops,* and *Opuntia.*

A certain resemblance may also be found between the *Cassia* hypodermal cells and the endosperm tissue in many palm seeds in which the thick walls contain hemicellulose that must be looked upon as storage carbohydrate. The function of the hypo-

dermis in *Cassia* is doubtful; by using the extraction procedure described by JENSEN (1962) the cell walls are clearly affected by ammonium oxalate. Especially a shrinkage of the middle parts of the thick walls had taken place. This, as well as a very deep coloration of the walls with Ruthenium-red suggest that great amounts of pectic substances are stored in the walls. After treatment with 17,5 % NaOH all wall structure disappeared, but a weak staining with PAS indicated that cellulose was present in small amounts, a fact which seems to agree with the results of NOMMENSEN cited above.

Pectic substances have a strong capacity of swelling, and therefore thick walls containing great amounts of such substances may act as water storage areas, which during periods of water shortage may be utilized by the green cells inside.

Inside the stomatal pores the hypodermis has narrow intercellular spaces surrounded by comparatively small cells (Plate VI a) which towards the cavity have cutinized walls. The substomatal chambers usually widen in the inner part of the hypodermis, but in some cases the hypoderm cells placed just inside the stomatal pore are Y-shaped and produce a shallow substomatal chamber between the two arms (Plate III c).

The thick-walled hypodermis is locally two-layered or its cell type is often imitated by some cells placed in the outer layer of palisade cells (Plate III c). The cells in question are elongate with thick brownish walls. In this way the palisade layer becomes interrupted by non-photosynthetic elongate cells. Sometimes the substomatal chambers continue in bell-shaped areas in the outer palisade layer. In such areas the intercellular canals between the cells are comparatively wide; they appear, therefore, lighter in thick sections (Plate III b).

Hypodermal cells may locally be converted into phellogen cells. In *Cassia rigida* a kind of ± roundish lenticels or short cork ribs are formed in the following way. In two opposite areas the hypodermal cells divide by radial walls. The cells facing the intermediate area are transformed into phellem cells thereby cutting off the hypodermal cells which they surround.

The hypodermal cells in the surrounded part are filled with dark brown substances before they die (Fig. 14 a). The phellogen expands from both sides and becomes finally groove- or bowl-shaped. In the center it may reach the sheath of crystal cells outside the fiber strands. Through the activity of the phellogen the cortex undergoes a dilatation and the epidermis is torn up. In the case pictured in Fig. 14 a some intercellular spaces occurred in the phellem making its lenticel nature probable.

Cortex inside hypodermis

There are two (three) layers of palisade cells which in most cases differ in the contents of crystal druses. As it appears e.g. from Plate III d druses are very abundant in the interior layers, while, they may be almost absent in the outer one. In *C. rigida* the interior palisade cells have a brownish contents. The innermost cortex layer is the sheath of crystal cells which accompanies the fiber strands (see Plate III d).

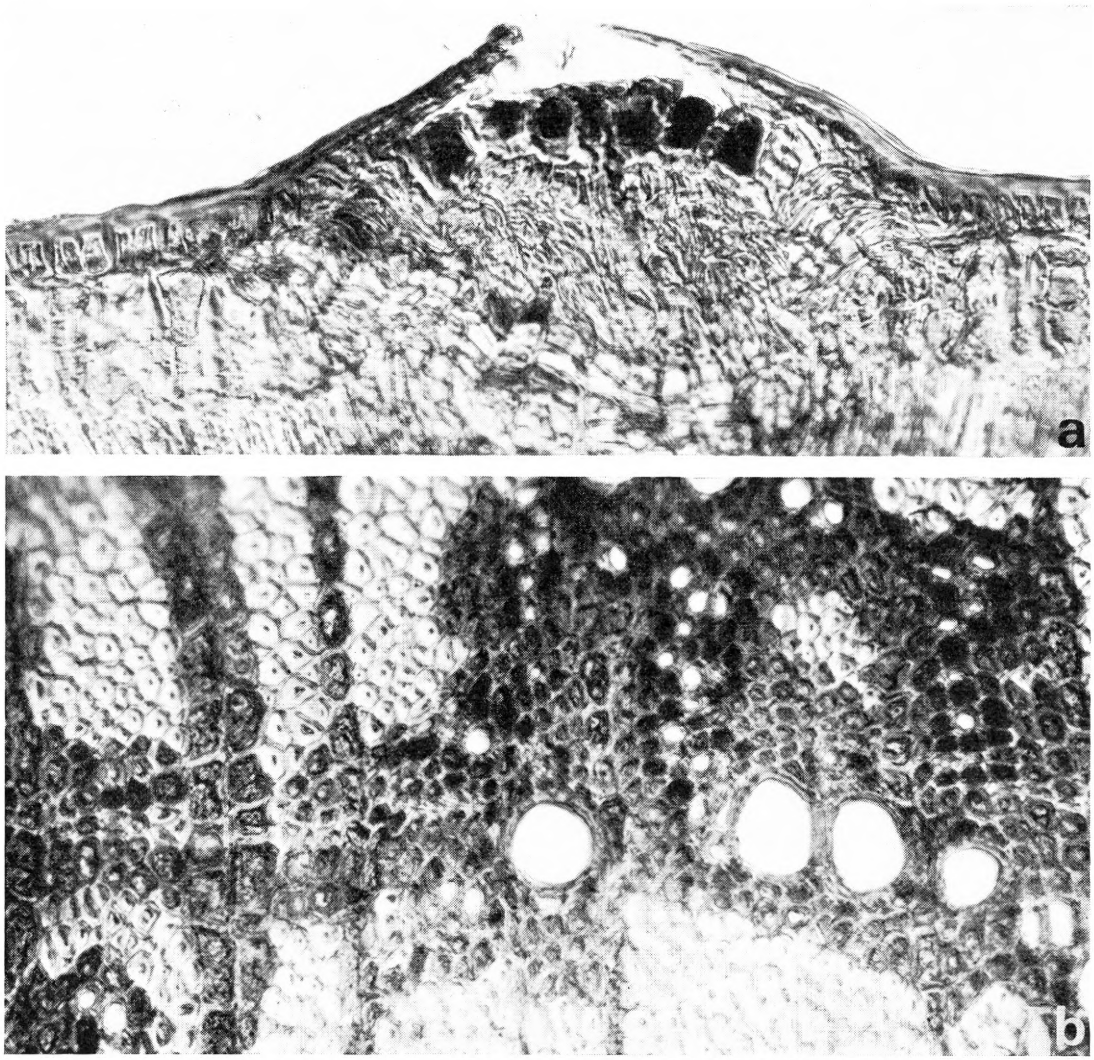


Fig. 14. *Cassia rigida.* a. Local phellem formation by which the epidermis is ruptured and part of the hypodermis isolated while the cells become filled with dark substances (tannin) (Sudan IV staining). — b. Transverse section of xylem showing banding of axial parenchyma which surrounds annual ring. Large vessels formed late (× 320).

Stele outside xylem

The strong fiber strands which are placed outside the primary xylem are connected tangentially by sclereids which, however, do not form a continuous layer.

Inside the fibers and sclereids follow first two, later three, cell layers of large parenchymatous cells. These cells may sometimes sclerify, but mostly their walls become rather thick and dark brownish, and some of the cells bear signs of obliteration. No doubt the parenchyma in question is connected with the primary phloem and

includes the obliterated remains of sieve elements. On the border between the large parenchyma cells and the secondary phloem some thick-walled elongate small cells occur which perhaps are primary phloem cells which are converted into fibers. At an early stage such fusiformed cells frequently divide into a row of small thick-walled cells (Fig. 6a). If the brownish parenchyma cells are dissolved, the space arisen by their solution would probably be filled with the expanding secondary tissues. A process of this kind would make an increase in girth possible for the secondary tissues without first requiring radical alterations in the cortex and the epidermis. We shall discuss this later in connection with the treatise of *Discaria articulata*.

The secondary phloem occupies a layer of different breadth, sometimes particularly distinct because of the brownish cell contents. In *C. rigida* the brown contents also occurs in the cambium cells and some of the xylem rays. The brown contents stains blackish with $FeCl_3$ and thus may be tannin. The phloem rays are usually dilated.

Xylem

The structure of the xylem varies. In most cases it appears uniform with but few larger vessels and uniseriate rays. In *C. rigida* and *C. crassiramea* biseriate rays are also found. The ray cells are frequently very rich in crystals. In *C. crassiramea* the axial parenchyma is banded and seems to contain elements which resemble cambium cells in structure, size, and position (Plate IIIe). No divisions were observed in these cells which may be interpreted as a relic cambial zone placed in a parenchyma band. Also in *C. rigida* the axial parenchyma is banded, paratracheal, and vasicentric-confluent. The wide vessels are formed late in the annual ring which is often surrounded by axial parenchyma and difficult to detect (Fig. 14b).

Pith

Often the pith contains crystals in the cells just inside the protoxylem. Sometimes crystal druses occur as well as cells with brownish contents (Plate IIIa). In older stems the cells in the perimedullary zone are radially elongate.

Discaria articulata (Phil.) Miers. (Rhamnaceae)

Material: Neuquén, W. Argentina, near San Martin de los Andes about 800 m. above sea level. Böcher, Hjerting & Rahn No. 1659. Dec. 14, 1955.

Occurrence and morphology

Discaria articulata occurs in Chile and Argentina from Northern Neuquén to Central Chubut and is an important member of a chaparral (or Macchi) vegetation which is developed on the border between the Patagonian steppe and the *Araucaria*- or *Nothofagus* woodlands in Southwestern Argentina. The marginal vegetation is often dominated by *Libocedrus* thickets, in which *Discaria* grows in clearings or in

small natural glades. At Lago Nahuel Huapi the *Discaria* chaparral contained e.g. *Adesmia boronioides*, *Fabiana imbricata* (cp. p. 48), *Diostea juncea* (cp. p. 89), *Anartrophyllum rigidum*, *Festuca pallescens*, *Mulinum spinosum*, and *Baccharis umbelliformis*.

Discaria articulata is an upright, 0.5–1 m. tall, densely branched shrub with decussate dark scale leaves supporting new branches. All branches terminate in spines. In the upper part flowering dwarf shoots appear. The short corymbose inflorescences have some green leaves, but in some scale leaf axils dwarf shoots are formed which have a dense almost rosulate leaf assemblage without flowers. Morphologically the scale leaves are leaf bases which may all originally have carried a small blade which was shed. The upright scale leaves are glabrous or have few short hairs on the underside (outwards facing) and many long white hairs on their upper side towards the axil. The surface of the internodia is glabrous. In some of the older parts almost all stomatal openings are provided with a small dark plug, the nature of which will be discussed below. Periderm is formed in the older parts of the green branches and covers small spots or larger parts.

Leaf anatomy

The leaf anatomy was studied by Pyykkö (1966:496) who classified the leaves among the *Acaena integerrima* type which has dorsiventral leaves with revolute margins. In our material the margins are not revolute and the stomata are not situated in furrows. Pyykkö mentions that some of the palisade cells contain tannin. In our material the palisade tissue is crowded with long tannin-containing cells. In certain areas these idioblasts (tannin-sacs) are so dense that the green cell rows in between become surrounded by the much larger brownish cells. The tannin-cells are light brown with the exception of one or a few ± spherical areas which are difficult to interpret. They may be vacuoles without tannin. They probably represent tannin-free parts of the central vacuole which for some reason keep clear of the dense tannin mass that occupies the major part of the vacuole, cp. Ledbetter & Porter (1970, Plate 9). Other much smaller tannin-cells accompany the vascular bundles. Near the underside tannin-cells are found in a hypodermal layer below the central vascular bundle. A similar distribution of tannin-cells is described by Pyykkö (l.c. fig. 61b) in another member of the *Rhamnaceae* viz. *Condalia microphylla*. Tannin-sacs in great number in the palisade tissue was described by Jönsson (1902 fig. 45), and Paulsen (1911 fig. 50) from the leaves of *Alhagi camelorum* (*Fabaceae*).

In *Discaria* leaves the stomata on the underside are not sunken. The cuticle is thin, but the outer epidermis walls contain a thin lamella which stains with Sudan IV. Near the substomatal chambers the inner walls are covered by a cuticle.

The scale leaves have a dark abaxial side and a hairy adaxial side. The transections available show that the dark colour is due to tannin which fills the cells in three layers below the epidermis. The cells in the epidermis have a thick cuticular layer which stains intensely with Sudan IV. The dark cells also have wall lamellae which

turn red, while the brownish masses remain unstained. The margins of the scale leaves are filled with similar brown cells, which also have suberin or cutin lamellae in their walls. On the adaxial side the epidermis cells have a very thin cuticle and many simple hairs which are cross-striated, built up by cellulose, and with a very narrow, empty lumen. Water draining down into the axil may possibly be absorbed as a result of capillarity of the hair cover and the activity of the living cells beneath.

Outline of stem anatomy

The epidermis is one- or two-layered and the stomata are sunken below the surface. A hypodermis of larger cells is present except beneath the stomata. The green cortex has 6–8 layers of palisade cells. On both sides of the phloem fibers a tissue of parenchyma cells with fairly thick and brownish walls is present. Phloem, cambium, and xylem form continuous cylinders around the pith (cp. Fig. 17a). Assimilatory stems also occur in *Discaria toumatou* Raoul, and are shortly described in METCALFE & CHALK (1957).

Epidermis

Already in young stems the outer walls are thick and heavily cutinized. From the cuticular layer cuticular flanges wedge in between adjacent epidermal cells (Fig. 15b, 19). Cutin and other wall substances may pass through micro-channels in the inner wall (Fig. 15b) and be deposited in concentric layers (Fig. 15c, d). The material produced by two adjacent cells outside their radial longitudinal walls accumulates to form long double-ridges which are conspicuous on the surface of the stem on SEM micrographs (Fig. 15a, Plate VIIa). However, in some cases a groove outside the middle lamella is formed. Obviously the wall is relatively weak here. Cracks in the cuticular layer, which are formed in connection with an increase in girth, will always occur outside the flanges and the middle lamellae.

In older stems the thickness of the outer walls increases about 10–15μ. During this growth the protoplast receeds but maintains a channel with a diameter of 1μ. This channel connects the micro-channels formed during the first wall formation with the protoplast (Plate VIId). Sometimes a single broad channel is replaced by several more narrow ones. On the surface of the cells wax deposits are observed (Plate VII), a fact which supports the supposition that the micro-channels work as pores through which wax precursors may flow. That part of the wall which is formed later reacts to Sudan IV (Fig. 18a, 19) as well as to periodic acid Schiff (PAS) and contains undoubtedly cellulose as well as cutin (Fig. 16d).

Between the stomata the epidermis usually consists of one cell layer only. But in the surroundings of the stomata it is two-layered. In these parts the epidermis swells and forms low cuticular ramparts (Fig. 15a, Plate VIIa).

The stomata are oriented with the pores transversally to the stem axis. The stomatal complexes are rather intricate. The are several narrow subsidiary cells inserted between the normal epidermal cells and the guard cells. They usually taper into a

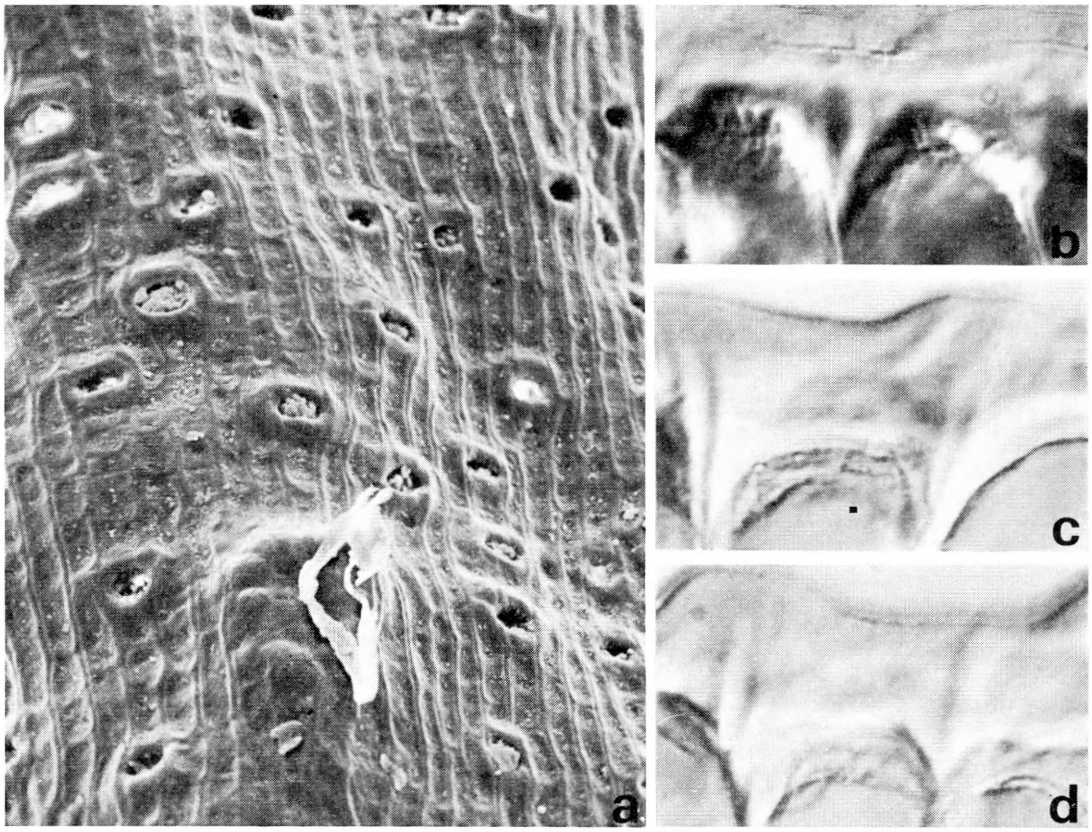


Fig. 15. *Discaria articulata.* a. Surface of stem. SEM micrograph showing cuticular double ridges overlying radial longitudinal walls and swellings around stomatal openings some of which are filled with fungal cells (× 195). — b–d. Cross sections of outer walls in young epidermis cells showing lamellation and radiating structures in cellulose layer (Interference contrast, in (b) Sudan IV staining, × 2000).

narrow part which overarches the guard cells and forms the side walls in a conical outer chamber. On top of the guard cells thick cutinized outer ledges enclose a front cavity. Then follows the stomatal pore which, however, is very much narrowed by two inner ledges which resemble the outer ones in size and form. These interior ledges develop outside the cells which are placed beneath the guard cells (Fig. 16a). The cells carrying the inner ledges belong to the inner epidermal cell layer and may be regarded as guard cell imitators. Owing probably to their position and development they have received some of the properties of the guard cells, but morphologically they show their relation to the guard cells only by assisting in the formation of the inner ledge. In old stems the inner ledges approach one another very much and may sometimes close the aperture (Fig. 16b). Even hypodermis cells adjacent to the substomatal chambers frequently produce some minute cuticular excrescencies (see Fig. 16b).

The walls which separate the guard cells and the underlying imitators get very

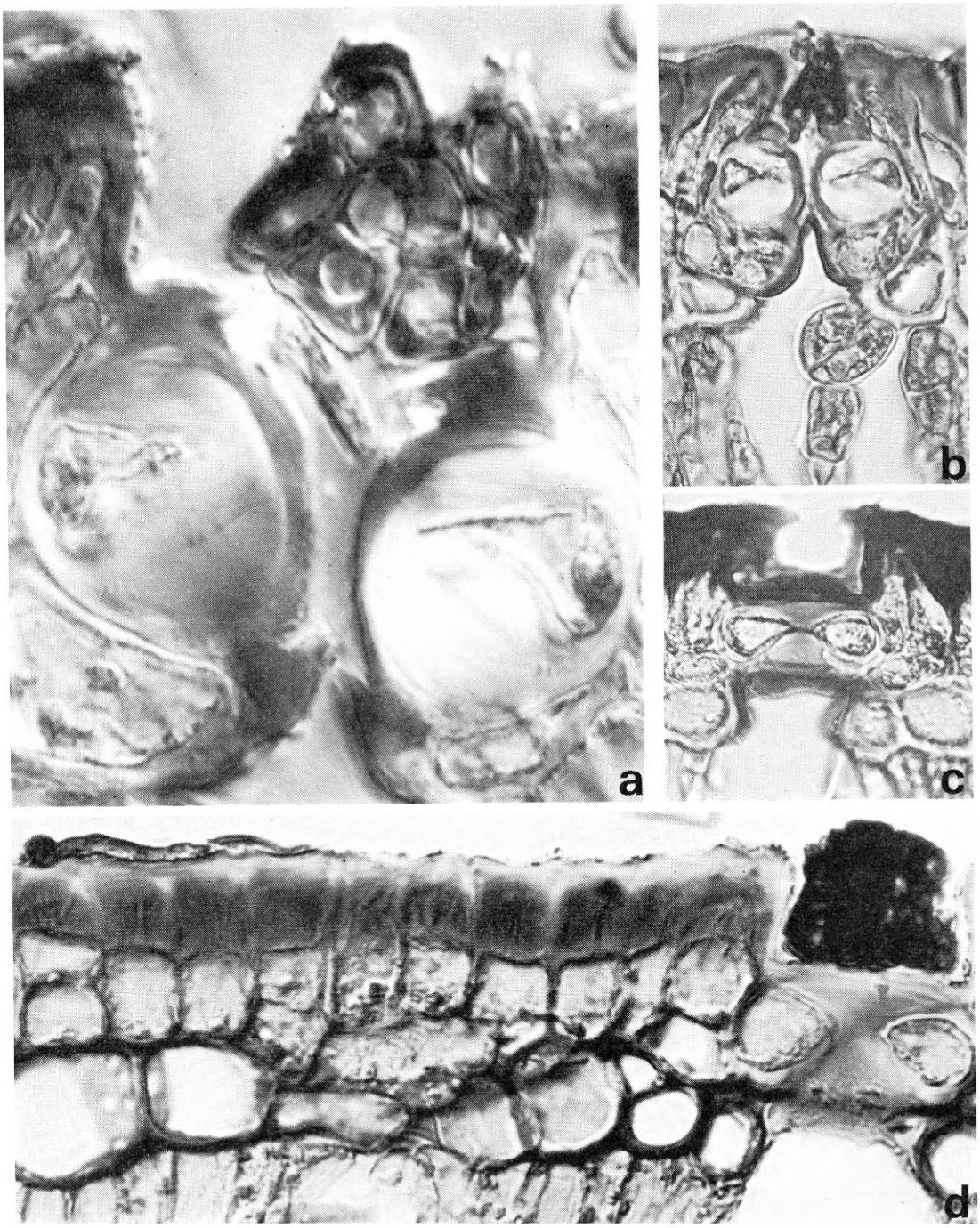


Fig. 16. *Discaria articulata*. a. Cross section of stomatal pore showing outer stomatal chamber with fungal cells. Walls towards the pore and outer and inner ledges cutinized. Thick outer and inner walls of guard cells lamellated (Sudan IV staining, × 2000). — b–c. Cross section and longisection of stomata and substomatal chambers stained with Sudan IV (× 500). — d. Longisection of epidermis and hypodermis, on the extreme right a stomatal pore with fungal plug. On the left one spore has germinated on the surface of the cuticle. The slide was treated with PAS which stained the cellulose walls and also the inner parts of the cuticular layer, which thus also contains cellulose (Interference contrast, × 800).

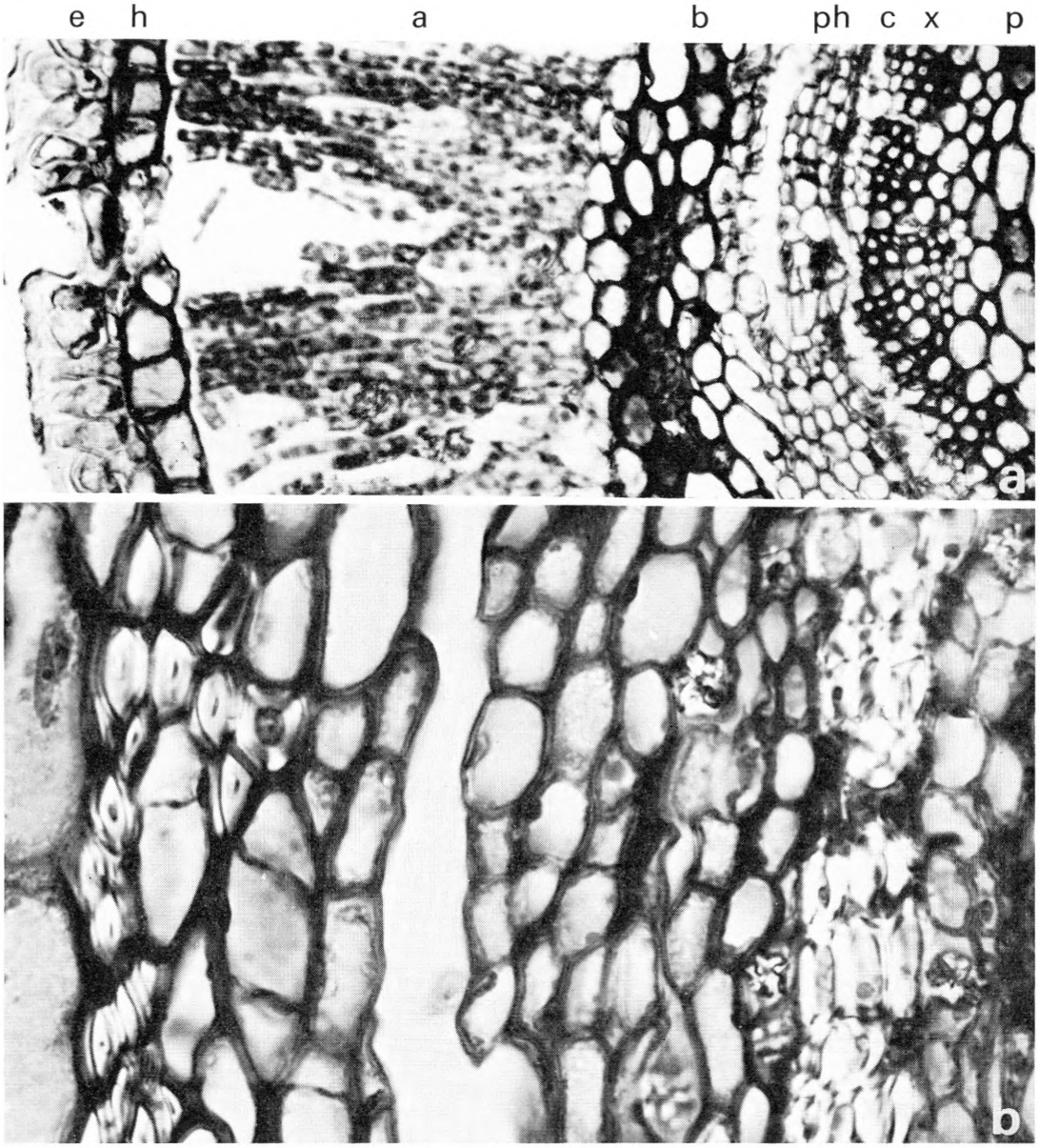


Fig. 17. *Discaria articulata.* a. Cross section of stem stained with Johansen's quadruple staining, one stoma cut; e epidermis, h hypodermis, a palisade tissue in cortex, b parenchyma with brown thick walls and phloem fiber strands, ph stratified phloem parenchyma, c vascular cambium, x xylem, p pith parenchyma (× 320). — b. Cross section of stem in partly polarized light to set off fibers and xylem cells. On the left side of the fissure primary cortex parenchyma surrounding fibers. Some of the cells with thick dark walls have divided into two or three smaller cells. On the right phloem parenchyma and xylem arranged in irregular oblique rows. Many cells with crystal druses (× 800).

thick making any kind of physiological interaction between these cells most unlikely (see Fig. 16a) The only wall which remains thin and flexible is the back wall distal to the pore. Even the walls facing the central part of the pore will in older stems increase considerably in thickness. The movements of the guard cells are, therefore, probably checked gradually, and the width of the pore greatly reduced.

A striking feature in *Discaria articulata* is the occurrence of fungal plugs in a considerable number of the outer stomatal chambers. The small fungal cell colonies are not uniform. In many cases they consist of many small thick-walled cells and larger cells with thin walls which are fewer in number. While fungal hyphae in some other species (see e.g. p. 127) penetrate into the cortex and are parasitic, this was probably not the case in *Discaria*. We saw hundreds of plugs but were not able to see clear signs of penetration of hyphae. Spores are produced and were in some cases seen germinating on the surface (Fig. 16d, on the left). The situation in *Discaria* resembles that found in *Monttea aphylla* (Böcher & Lyshede 1968), where the fungal cells may utilize carbohydrates which seem to be produced by the epidermal cells and reach the surface.

In *Discaria*, however, the outer parts of the cuticular layer does not seem to contain carbohydrates. Hence, a similar activity of the epidermal cells is not probable. Another explanation would be that the fungal cells might utilize some kind of organic substances which were produced in the stem and liberated together with aqueous vapour when the stomata open.

We have used the term "plug" in order to point out that dense colonies of fungal cells most probably will reduce the transpiration rates from the stems. In fact we may be faced with a peculiar and special kind of symbiosis which deserves further study.

Cortex and periderm

Areas of varying size in the stem are frequently covered by cork. Phellogens are initiated in the epidermis as well as in the hypodermis (Fig. 18). The phellem layers may be thick, but also a considerable amount of phelloderm cells are produced and contribute to the dilatation of the stem section beneath (Fig. 18b).

The hypodermis is made up of large cells with fairly thick walls. The cell size, however, is greatly reduced in the parts adjacent to the substomatal chambers where the hypodermis is interrupted (Fig. 16, 19). Occasionally single periclinal walls are formed making, very locally, the hypodermis two-layered.

Most of the cortex is occupied by a uniform green palisade tissue in which some of the cells contain crystal druses. Apart from the wide and deep substomatal chambers the palisade tissue has narrow intercellular spaces. This character, as well as the occurrence of a hypoderm, is shared with another member of the *Rhamnaceae* viz. *Colletia spinosissima*, see p. 41. In the internodes there are usually 7–8 layers of palisade cells and a single internal layer of green ± isodiametric cells. However, near the nodes the number of layers decreases to 2–4 and the exterior green cells become wider.

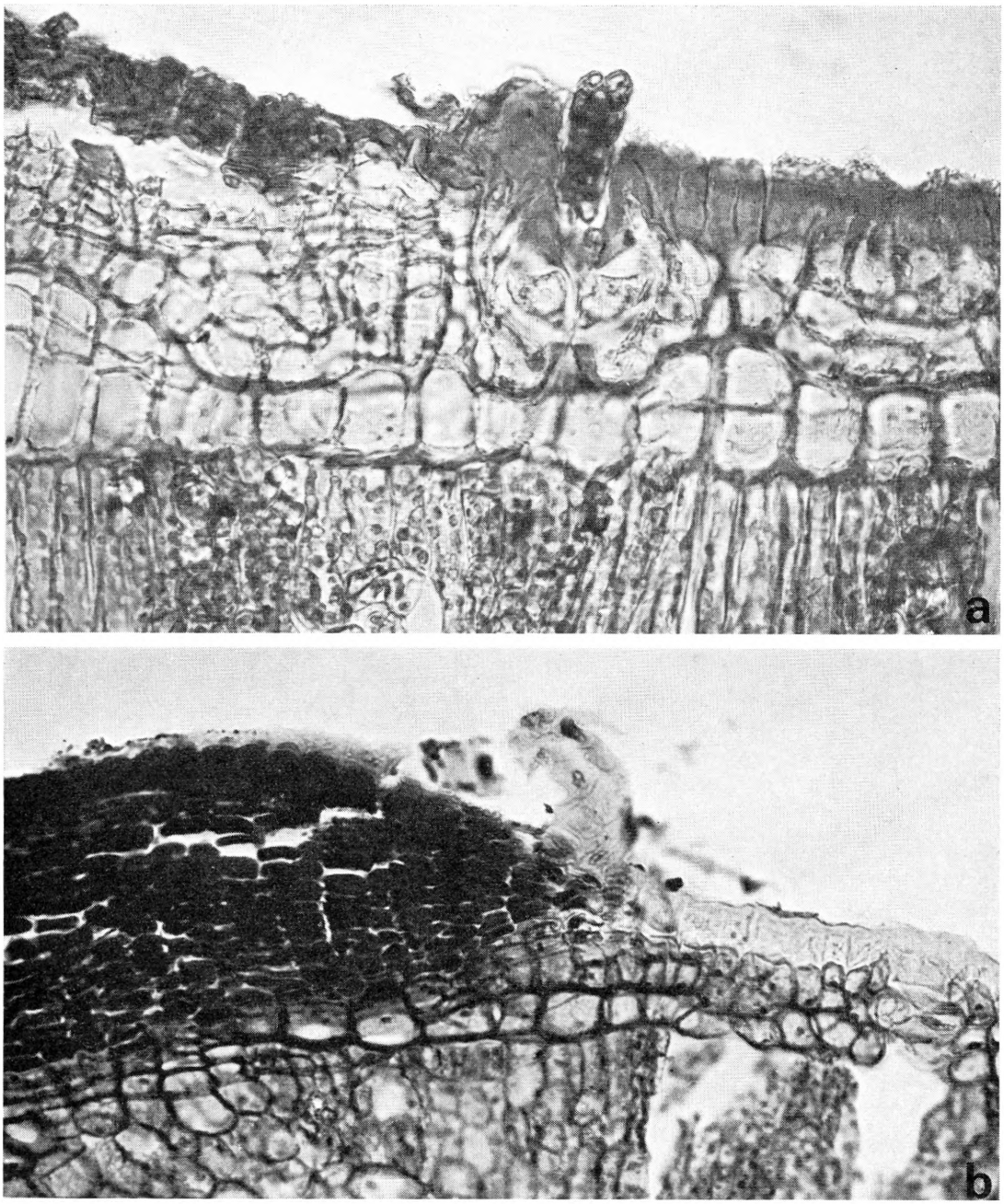


Fig. 18. *Discaria articulata.* Periderm formation in older stem. (a) stained with Sudan IV, (b) with Safranin-Fast green. The phellogen is initiated in the epidermis and the hypodermis which are divided by tangential walls. — a. Front cavity of stomatal opening filled with fungal plug, substomatal cavity still present. On the right the long central channels in the outer walls of the epidermis cells are visible (× 500). — b. On the right two substomatal cavities, phellogen formation just initiated. On the left a thick phellem layer has been formed and also several phelloderm layers (× 320).

Stele

The phloem fibers and the surrounding parenchyma cells raise a number of questions. The parenchyma cells occupy 4–6 layers of cells, and the fibers occur inside the first or the second layer. The parenchyma cells are of varying sizes but are often large, and some of the big ones may be divided at a late stage into two or three cells (Fig. 17 b). Many of the cells have brownish and thick walls and in some of the branches they seem to die or be decomposed early. In sections stained with Sudan IV their walls contain two lamellae, one on each side of the middle lamella, which seems to be stained

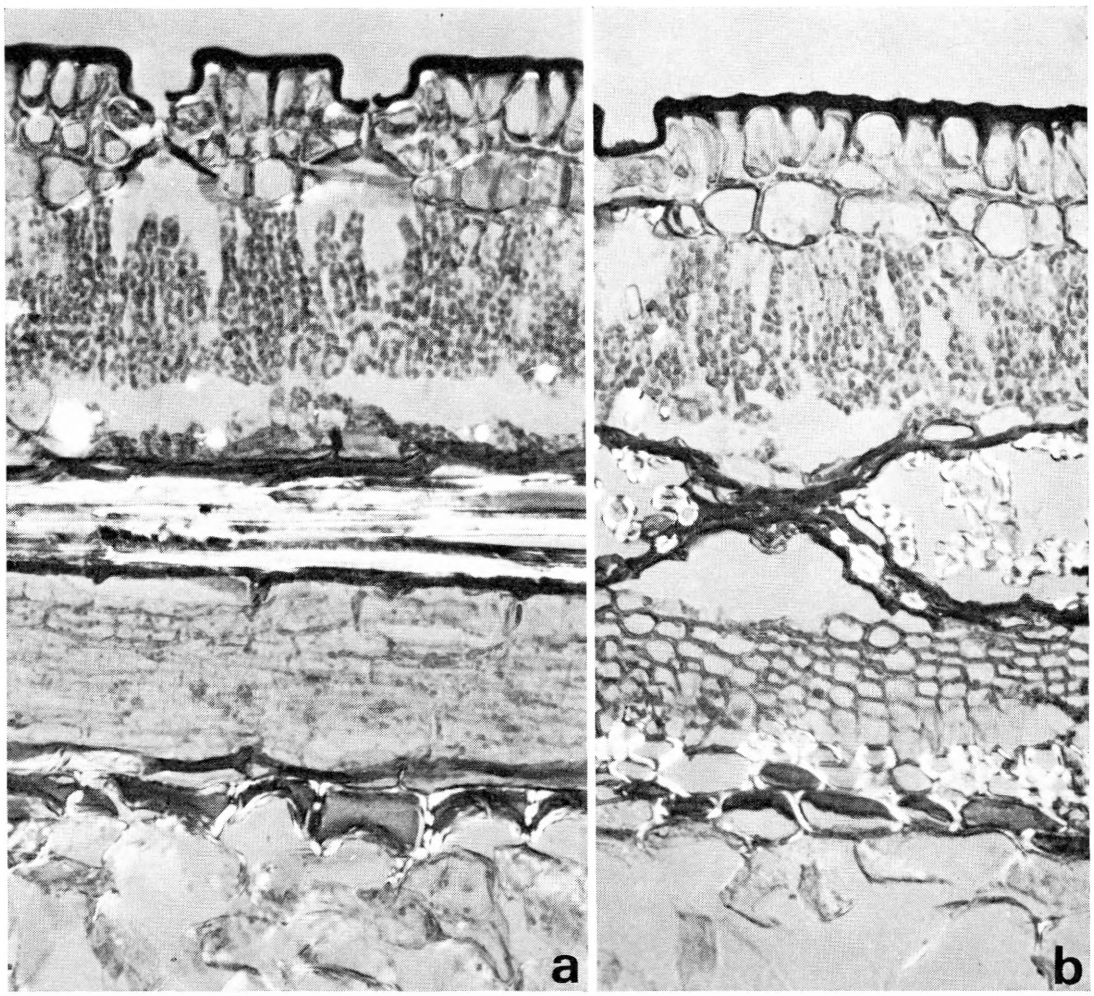


Fig. 19. *Discaria articulata*. a. Radial (longitudinal), b. Cross (transverse) section of stem stained with Sudan IV and photographed in half-polarized light. Transverse section of two stomata in (a), and longitudinal section of one stoma in (b). Under the epidermis, which sometimes has two cell layers, is a hypodermis of large parenchymatous cells. Next follows a cortex palisade tissue, phloem fibers surrounded by partly decomposed cells with thick brownish contents, phloem, cambium, xylem (in b), one to two perimedullar cell layers with thick brownish contents, and finally thin-walled pith parenchyma (× 320).

and may be suberized. The cells resemble the brown cells in the scale leaves by their staining properties and also by their brownish contents which probably is due to tannin. Some of the parenchyma cells and the fibers may have replaced the primary phloem which was absent in the material studied. During the obliteration of the cells a number of stages or different processes may be singled out:

(1) *Dissolution of transverse walls.* In longitudinal sections transverse walls in the parenchyma cells bordering phloem fibers are dissolved. The walls stay narrow but are finally dissolved, the dissolution starting from the middle of the cell. During this process the wall is split into at least four lamellae, two on each side of the middle lamella. The exterior pith cells bordering the xylem (the medullary sheath, Fig. 20c, Plate VIIIe) behaved in a similar way.

(2) *Swelling of the middle part of the wall.* This phenomenon preceeds a dissolution of the wall. At the first stage a number of small swellings appear (Plate VIIIc). The middle part is transformed into a homogeneous substance in which a line corresponding to the position of the middle lamella is still visible. On both sides the swellings are surrounded by two lamellae (Plate VIIIc) which burst when larger bladders are formed.

(3) *Decomposition of cell contents.* The dissolved wall substances may be mixed with the dying cytoplasma and gather as brownish masses along walls which are not dissolved. Especially in corners the brownish mass is deposited (Fig. 20b, c, Plate VIIIb). The mass seems to be very delicately striated transversally to the direction of the wall beneath. Brownish masses along two opposite walls merge when the cells are exposed to some kind of pressure (Plate VIIIa). Following the extraction procedure worked out by JENSEN (1962), the brownish masses were unaffected by 4% NaOH, but disappeared almost entirely with 17,5% NaOH. They may contain some carbohydrates which arose by the decomposition of cellulose and were dissolved by the strong NaOH. The brown colour is due to tannins. The brown masses and cell walls were stained blackish when treated with $FeCl_3$.

(4) *Crushing of cells.* At an early stage the cells may be exposed to pressure from the expanding secondary tissues which develop centrifugally, and perhaps also from the cortex parenchyma which seems to increase its number of cell layers. As some of the brown walls are maintained together with the brown masses, a peculiar resistant brownish sheath is formed in which phloem fiber cells are embedded or which surrounds phloem fiber strands. In some of the material the brown sheath surrounded fiber strands as well as empty cavities (Fig. 19) which probably develop after dissolution of most of the primary phloem.

The cavities shown in Fig. 19 are probably to some extent artificial and due to the microtoming which is difficult to perform in material of this kind. But even artificial splits as those seen on Fig. 17b are found just on the border between the secondary and the primary phloem. This fact indicates that the secondary tissues, when they expand,

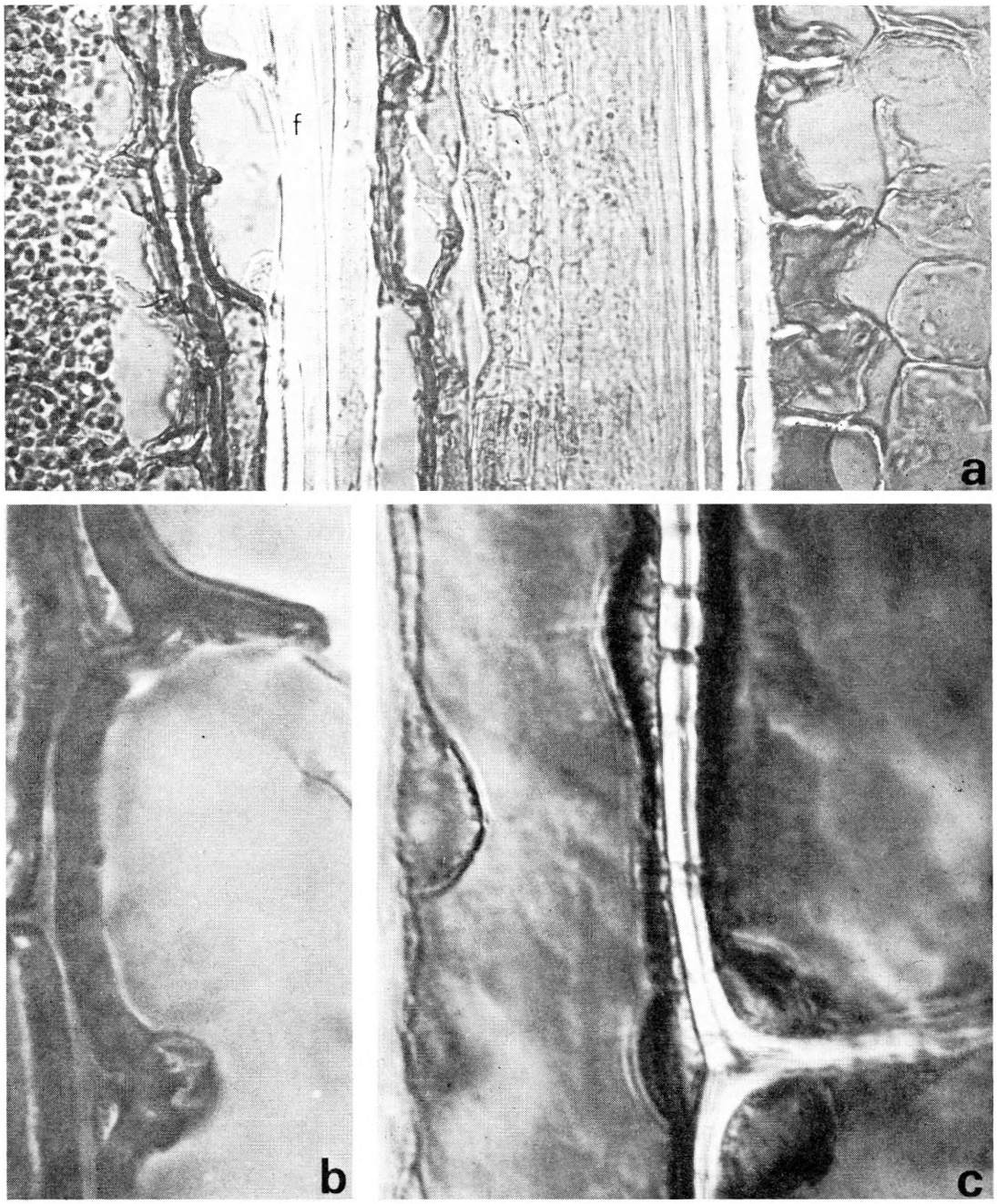


Fig. 20. *Discaria articulata.* a. Longitudinal section in half-polarized light from the left showing palisade cells, brownish walls in decomposed cell layer interrupted by fibers (f), phloem, cambium, xylem, perimedullary cells with brownish walls, and normal thin-walled pith cells (× 500). — b. Part of (a) showing brown masses deposited on both sides of cell wall (× 2000). — c. Part showing pits and middle lamella as well as brown masses which are deposited in cell corners, dissolution of the transverse wall is taking place (Staining with PAS, interference contrast, × 2000).

meet and push the primary ones, while the cells from both sides are not being connected. As far as the dilatation growth in *Discaria* is concerned it may be of importance that the secondary tissues are fairly expandable in areas left open by the dissolved primary phloem parenchyma. This expansion can proceed without influencing the green cortex and the epidermis. A similar development will be mentioned later under the discussion of *Neosparton aphyllum*.

The secondary phloem is to a great extent made up of parenchyma cells. The cambium produces great quantities of these cells which on longisections appear to be storied. Some of the cell layers become filled with crystal druses. In stem sections close to the nodes there may outside the cambium be 5 layers of phloem parenchyma followed by 3–4 layers of sclerenchyma and a number of phloem layers with radial rows of druse-containing cells.

The xylem is markedly reduced. In a stem with well developed cortex most parts of the xylem is not mature. The xylem has 1–2 seriate rays. Fibers are abundant. Large vessels occur scattered or in irregular tangential bands. The growth rings are indistinct and frequently starting with fibers. The connections between the photosynthetic cortex and the conducting tissues appear to be made difficult by the brown sheath, but outside the rays one finds gaps in the sheath formed by the brownish cells and the fibers associated with them.

On the border to the xylem the pith has a medullary sheath of cells with brownish contents (Fig. 19). The ray cells as well as the pith parenchyma may be filled with starch grains. However, in some parts of the material crystal druses also occur in great quantities in the pith. With increasing age the pith parenchyma cells develop thick walls.

Colletia spinosissima Gmel. (Rhamnaceae)

Material: W. Argentina, Neuquén, San Martin de los Andes, 40° lat. S. 800 m. above sea level (Böcher, Hjerting & Rahn No. 1698, Dec. 15, 1955). Additional material originating from Chile and collected in a botanical garden under the name *C. ferox* Gill & Hook. (a synonym for *C. spinosissima*). The latter material is referred to as the Chilean.

Occurrence and morphology

Colletia spinosissima occurs in Chile and W. Argentina (from Santa Cruz to Tucumán). Our material from Neuquén was collected on a dry north-facing rocky slope at a great lake. It grew in thickets of *Austrocedrus chilensis* and together with shrubs like *Embothrium coccineum*, *Lomatia hirsuta*, and *Discaria articulata*. In Chile it forms a kind of dry dwarf shrub heath in old dunes at some distance from the Pacific (*Colletia spinosissima—Neoporteria subgibbosa*—community described by Kohler 1970).

C. spinosissima reaches a height of 0.5–4 m. It is densely branched and all branchlets terminate in thorns. Flowering shoots occur above dwarfish thorn-shoots. Thus,

two seriately placed shoots are in such cases supported by the same leaf. The ovate-lanceolate leaves, few in number, are 2–4 mm long and placed on the main axis. At their bases there are narrow, lanceolate, tapering, dark stipules which remain, while the rest of the leaf is shed. Also the scale leaves which occur in the lower part of the shoot are dark and persisting. In the upper part the stems are slightly furrowed and have projecting hairs, whereas they are almost glabrous below. The thorns may have some small hairs which are shed very early. We agree with ESCALANTE (1946) in regarding the species as being very polymorphic. The two collections available to us differ from one another in a number of anatomical characters.

Outline of stem anatomy

The green cells are covered by a hypodermis and a single-layered epidermis. The chlorenchyma is very dense and consists of 5–6 cell layers of which the outermost has the character of a palisade tissue. The contents of crystal druses increases in the inner layers where some of the cells contain tannin. A number of schizogenous cavities also occur here. The innermost cortex layer clearly corresponds to an endodermis and is followed by groups of perivascular fibers. The cells here have large primary pit fields in horizontal walls. Next follows a parenchyma of rather large cells with contents of starch, then, on the border to the secondary phloem but only in the Argentinian material, two or more layers of sclerenchymatous cells all of which usually contain a prismatic crystal.

The secondary phloem also contains druses and sometimes a great many starch grains. The phloem rays are uniseriate, sometimes biseriate or even triseriate. The outermost cells increase in size. The xylem rays have 1–3 (4) cell rows of quadrate or upright cells which often contain crystals. The wood appears to be storied, and the larger vessels are arranged in radial aggregates along the rays. Axial parenchyma seems to be very sparse, a circumstance which may be compensated by the very numerous rays. The fibers occur in broad bands almost without vessels.

The pith consists of very wide cells mostly with thin walls, but in the Chilian material some of the cells have thick walls and sometimes contain tannin.

Regarding the occurrence of pith flecks in the Argentinian material see below.

Epidermis

As observed in the scanning electron microscope the Chilian material deviates from the other by having a surface structure which is much more irregular owing to the occurrence of ± loose wax crusts and scales. There are many cracks which obviously are formed mainly outside anticlinal axially stretched walls. In this material it is hardly possible to detect the stomatal pores. The long axis of the guard cells is placed at right angles to the axis of the stem, and some of the cracks are undoubtedly formed outside the narrow extra front cavities formed by the overarching subsidiary cells (Fig. 21b and c). In the Argentinian material narrow chaps in the cuticular surface are clearly formed over the stomatal pores; sometimes two parallel chaps are found on

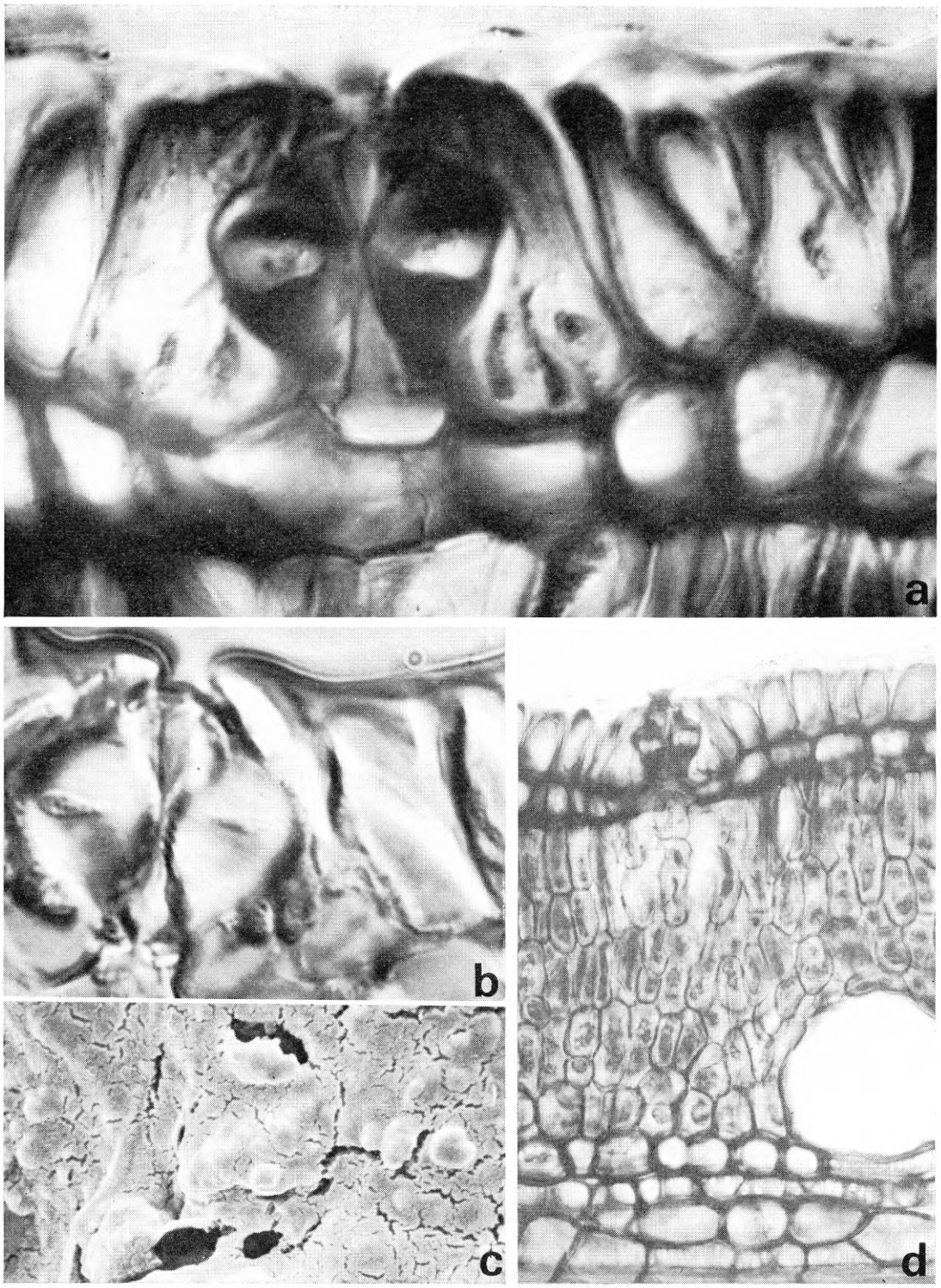


Fig. 21. *Colletia spinosissima.* Material from Chile. a–b. Stomatal apparatus as seen in longisections of stem. — a. Quadruple staining and interference contrast. Hypodermal bridge below back cavity, long cuticular flanges, dark-stained interior walls of guard cells (× 2000). — b. Safranin-Fast green staining and interference contrast showing furrowed walls towards central pore (× 2000). — c. SEM micrograph of surface of stem; wax covering cracked and with irregular openings above small extra front cavities (× 2100). — d. Outer part of stem, longisection. Abaxial palisade cells entering substomatal space in hypodermis. Very dense palisade tissue, schizo-lysigenous cavity outside sheath (endodermis) and three layers of parenchyma bordering phloem fibers at bottom of the picture (× 500).

both sides of the pore which may be filled with granular material (probably wax). As appears from Fig. 22d and 23a the overarching by the subsidiary cells in the Argentinian material is not pronounced. There is hardly any extra front cavity, but two parallel grooves on the border between the subsidiary cells and the guard cells clearly corresponding to the two parallel chaps. The guard cells are provided with low outer and inner ledges and consequently small cavities are formed on both sides of the pore. The substomatal chamber is often narrowed by hypodermis cells which bridge over the chamber (Fig. 21a) or by palisade cells which fill the chamber from below (Fig. 23a). On both sides of the guard cells there are usually three closely connected subsidiary cells. Apart from the back walls towards the subsidiary cells the walls of the guard cells grow very thick and are stained dark by Johansen's quadruple stain. This is particularly the case with the inner walls proximal to the cell lumina. Sudan IV stains the secondary thickened outer walls of the guard cells. The inner walls taper towards the substomatal chamber. The walls facing the pore (Fig. 21b) are provided with parallel grooves (cp. *Fabiana* p. 54).

The cutinization of the walls of the normal epidermal cells is extensive and includes the greater part of the outer thick walls, the anticlinal walls with the thick flanges, and even larger parts of the thin inner walls. Some of the anticlinal walls in the, hypodermis are also cutinized in their outer part.

A very conspicuous system of micro-channels issues from the outer parts of the cells. The micro-channels become dark-coloured by treatment with Johansen's quadruple stain (Fig. 23) and very clear when using interference contrast (Fig. 22). They traverse clearly the latest formed inner parts of the walls but may likely continue towards the cuticle as submicroscopical channels. Considering the great amount of wax on the surface we assume that the delicate structures function as channels for wax precursors which ooze towards the surface.

Pith flecks

In parts of the Argentinian material pith flecks had developed in a crack formed near the first annual ring. The pith fleck did not form a continuous cylindric layer. A small sector of the xylem was intact. The crack might have been caused by frost or extreme desiccation. In one end the crack was filled with a brownish mass probably formed as a result of gummosis of the cell walls in dying cells bordering the crack. The rest of the crack was entirely filled up with parenchymatous cells which were in close connection with some of the xylem rays. Undoubtedly the pith fleck had been filled up with cells originating from the rays. During the development the pith fleck parenchyma had pressed the brown masses resulting from gummosis against both sides of the old xylem, and it therefore appeared as if it was lined with very thick brown walls. The cell walls of the pith fleck parenchyma are lignified and rather thick, and almost all cells contain a crystal. In some parts of the crack the brown bordering gums also delimit the pith fleck parenchyma towards the rays on both sides. The latter had become displaced in relation to one another during the filling out period

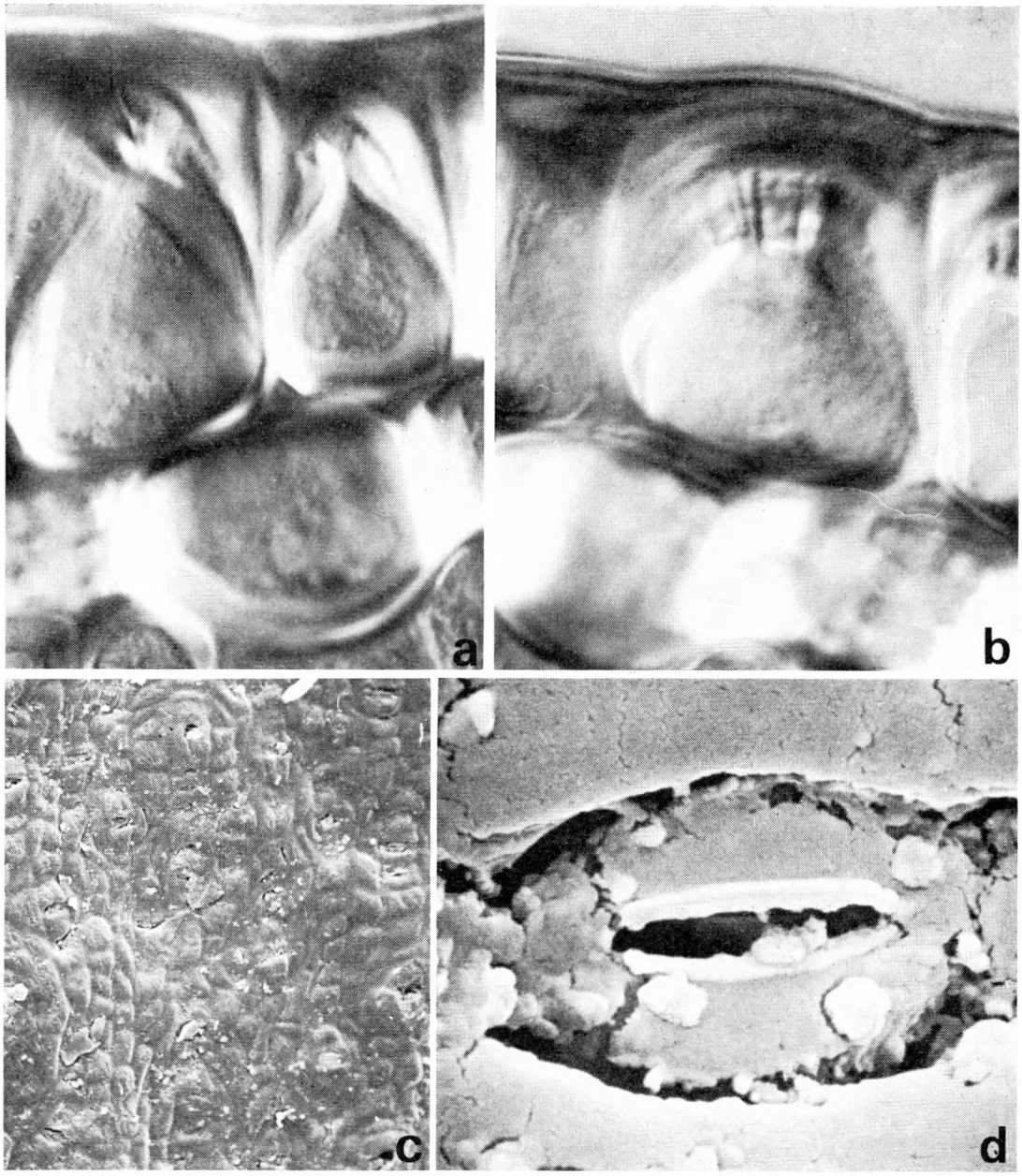


Fig. 22. *Colletia spinosissima*. Material from Argentina. a–b. Epidermis cells, interference contrast observations showing wall lamellation and radiating strands through inner part of outer wall. — c. Surface of epidermis (SEM micrograph, × 210). — d. Stomatal opening with grooves on both sides between guard cells and the cuticular layer covering the subsidiary cells, see Fig. 23 (SEM micrograph, × 5250).

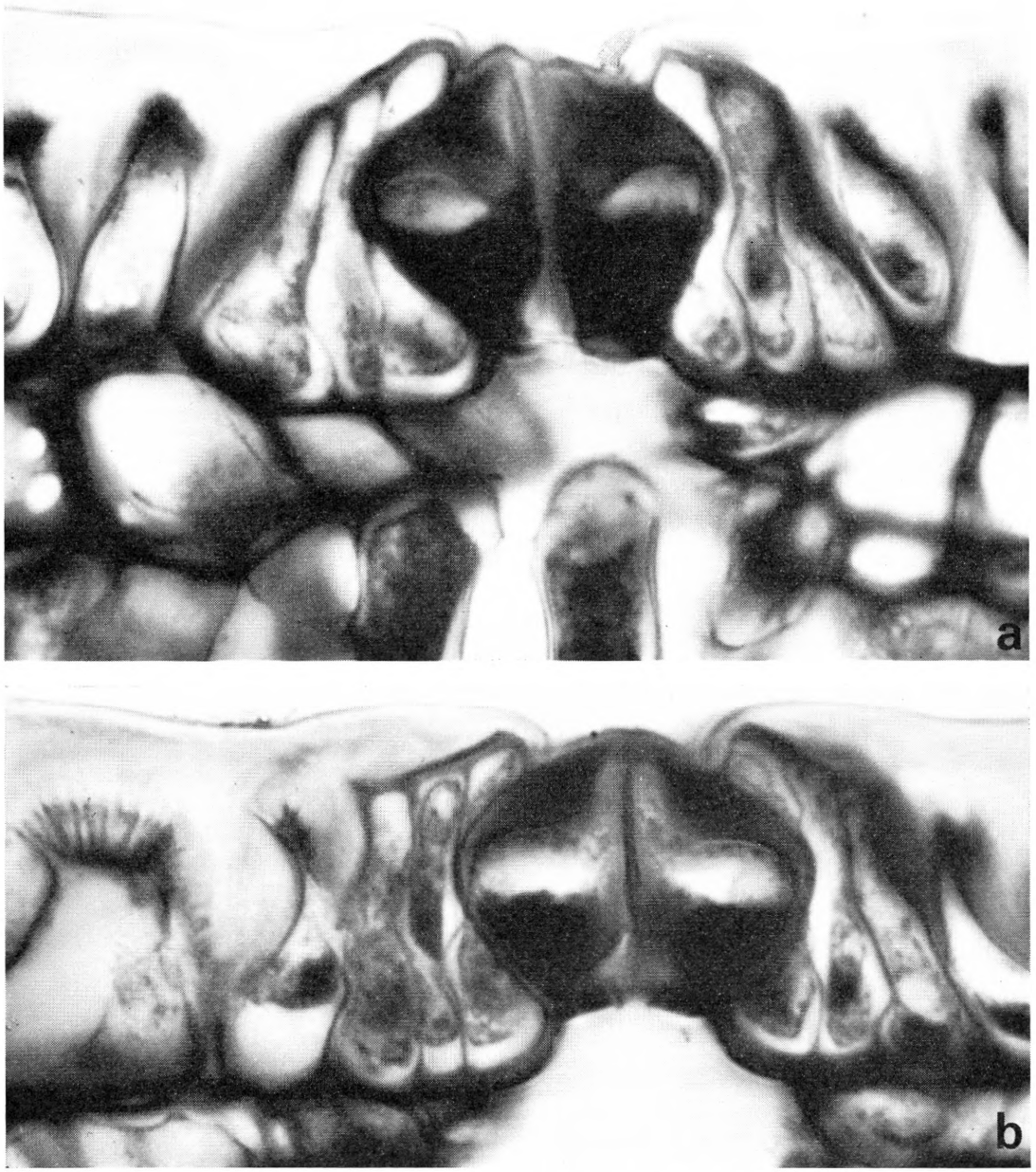


Fig. 23. *Colletia spinosissima.* Material from Argentina. Stomata with surrounding groups of subsidiary cells. Numerous radiating ectodesmata (micro-channels) from outer part of epidermis cells. Inner thick walls of guard cells stained very dark. Substomatal cavity in (a) partly filled with palisade cell (Quadruple staining, × 2000).

of the crack, and the rays outside the crack nearest to the bordering gums had increased in breadth not only by adding to the size of the cells but furthermore sometimes by increasing the number of cell rows.

Menodora decemfida (Gill. ex Hook. et Arn.) A. Gray (Oleaceae)

Material: W. Argentina, Mendoza Prov. 5 km below Villavicencio, 1500 m. above sea level. Böcher, Hjerting & Rahn No. 2107, Jan. 6, 1956.

Occurrence and morphology

Menodora decemfida is a 20–75 cm tall, almost glabrous, half-shrub. It is distributed in the Provinces Catamarca, La Rioja, San Juan and Mendoza in NW. Argentina (Meyer 1957, map on p. 212). It occurs in Monte shrub steppes and is an important member of the dry rock vegetation. At La Quebrada de Villavicencio which was described by Roig & Roig (1969) it dominates the sunny slopes facing north, its co-dominants being *Dipyrena glaberrina, Stipa ichu* or *Artemisia mendozana.* The material collected for anatomical studies grew abundantly together with *Artemisia mendozana, Echinopsis* cfr. *formosa,* and a species of *Opuntia* with large yellow flowers.

Menodora decemfida is not apophyllous but it approaches the leafless shrubs by a rather early shedding of the stem leaves and by the green stems. The opposite leaves are lanceolate, 6–15 mm long and 1–3 mm wide, sometimes mucronate. The green assimilatory internodia are 1–5 cm long. A description and drawing of the plant is found in Meyer (1957 pp. 218–220).

Leaf anatomy

The leaves are isolateral approaching a dorsiventral structure. Along the margins they are provided with scattered, short, curved hairs. Short papillate hairs are found mostly on the upper side. This is also the case with the glands which are particularly frequent near or in a shallow furrow above the middle vein. In this character they resemble leaves of *Junellia glauca* (Fig. 44a). The glands are always placed in small depressions and seem to be sessile when seen from above. However, they have a short stipe which fills out the depression and a head of four cells (Fig. 24a). The epidermal cells often contain crystal sand.

At the leaf margins the outer palisade cells frequently sclerify; the same is the case with the cells between some of the vascular bundles and the epidermis. Neighbouring cells to these sclereids often increase in size and die while at the same time their walls become suberized.

Outline of stem anatomy

The stem has four ridges. Two pairs of such ridges are placed on opposite sides of the stem surrounding two broad and shallow furrows. The furrows begin where two opposite stem leaf bases approach one another. They run through the whole

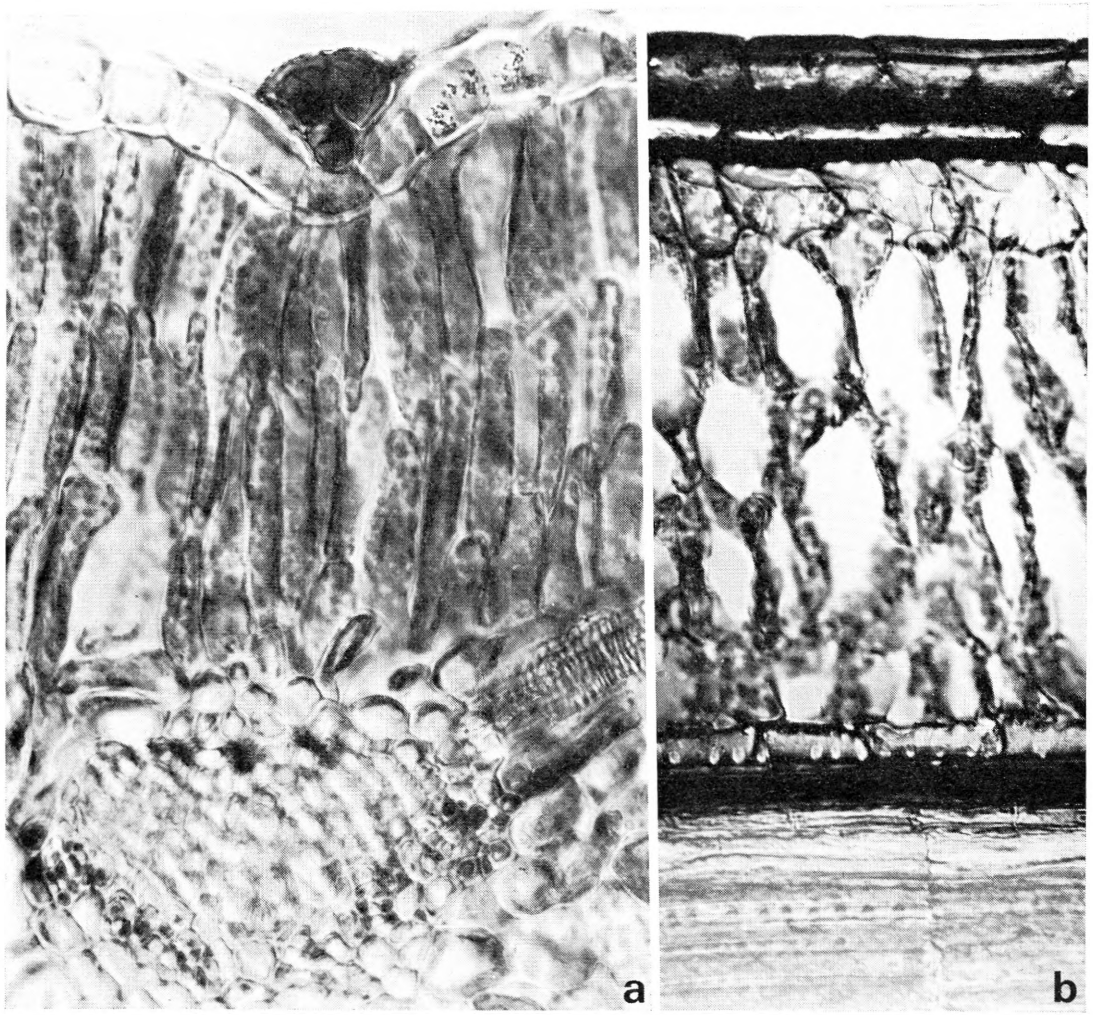


Fig. 24. *Menodora decemfida*. a. Cross section of leaf showing gland situated in furrow above middle vein. On the right lateral vein; crystal sand in some of the epidermis cells (Safranin-Light green staining, × 500). — b. Longisection of stem. Epidermis, hypodermis (thick black walls). Outermost chlorenchyma cells densely spaced and increasing very much in breadth towards hypodermis. Inner photosynthetic tissue palisade-like, plasmolyzed and with large intercellular spaces. Endodermis very distinct with large oval simple pits. Dark-stained fiber outside phloem and xylem (× 500).

internode below. On transects the four ridges are supported by collenchyma. Inside a typical hypodermis the green cortex has several layers of palisade cells. In the endodermis the radial walls have large oval primordial pits in which plasmodesmatal pores are readily visible in the light microscope. Numerous groups of perivascular fibers occur in a layer inside the endodermis which surrounds cylinders of phloem and xylem. The pith has large cells with lignified walls. The xylem fibers have very thick walls. The vessels are small and scattered.

Epidermis

The most deviating feature may be the occurrence of lamellae in the inner parts of the outer walls which stain with Safranin. In normal epidermis cells these lamellae which probably are lignified occur inside the cuticular layer. In the same areas which may contain lignin micro-channels occur or seem to be particularly dense. Also the wall thickenings in the collenchyma as well as thickenings between epidermal and hypodermal cells may lignify (see further Fig. 24b). It appears to be the wall sections containing pectic substances which undergo lignification.

The guard cells are not sunken at all or only very slightly, as a result of some bulging of the subsidiary cells. Sometimes they may even appear raised because the subsidiary cells bulge outwards. This was noticed in some of the stomata situated in the two furrows. The outer ledges protrude and cover a front cavity. The inner ledges are very small. In side views of the guard cells many micro-channels are observed radiating into the outer ledges. All stomatal openings are arranged with their long axis parallel to the main axis of the stem (Fig. 25a). Safranin stains the walls lining the stomatal pore, and frequently also the walls separating the guard cells from the subsidiary cells (Fig. 25d).

On the surface of the stem there are scattered papillate cutinized hairs (see Fig. 25b). In the sections studied by us there were few hairs in the two furrows. But on dried specimens from Mendoza some short white hairs occurred and possibly also glands of the same type as those found on the leaves. In material collected by Hawkes, Hjerting & Rahn No. 3153 at lat. 32° 32′ S. the younger internodes were hairy at the base and had white short hairs.

The furrows which terminate above the bases of the next leaf pair may lead water down to the node where it may be taken up by hairs placed on the leaf bases and by the axillary buds which are covered by hairs. Water uptake has been demonstrated to take place in furrows in the upper part of the middle nerve in *Fraxinus* leaves and might also take place in *Menodora decemfida* which is another member of the *Oleaceae*.

Fabiana viscosa, F. denudata and F. imbricata (Solanaceae)

Material: The structure of these three species shows great similarity, a fact which makes it natural to treat them together.

Fabiana viscosa Hook. & Arn. Mendoza Prov. W. Argentina, Atuel valley, near Arroyo Blanco, 1770 m. above sea level. Hjerting & Rahn No. 3084, Dec. 22, 1965.

Fabiana denudata Miers. The same locality as the preceeding. Hjerting & Rahn No. 3083, Dec. 22, 1965. Further Arroyo de las Papagayos north of the Atuel valley. Böcher, Hjerting & Rahn No. 2072, Jan. 3, 1956.

Fabiana imbricata Ruiz & Pav. Rio Negro Prov. W. Argentina, near Nahuel Huapi. Böcher, Hjerting & Rahn No. 1720, Dec. 15, 1955.

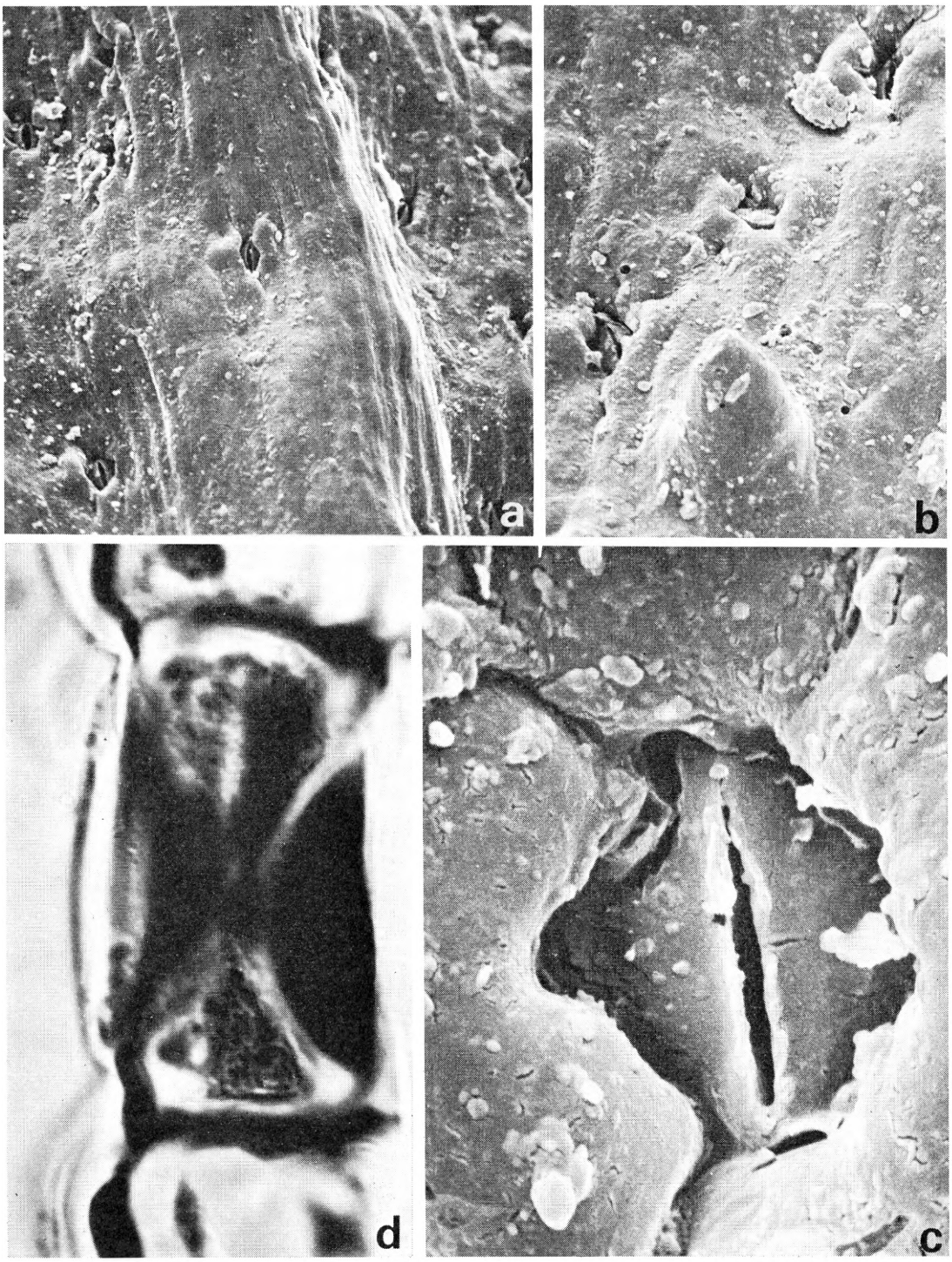


Fig. 25. *Menodora decemfida.* a–c. SEM micrographs of stem surface and stomatal openings. (a) showing rib (× 205), (b) a papillate hair (× 400) and (c) a stomatal opening (× 2060). — d. Guard cell, lengthwise, treated with Johansen's quadruple staining; interior part of outer walls in epidermis cells, parts of radial walls and walls of inner front cavity and entire back cavity stains dark reddish indicating lignification (× 2000).

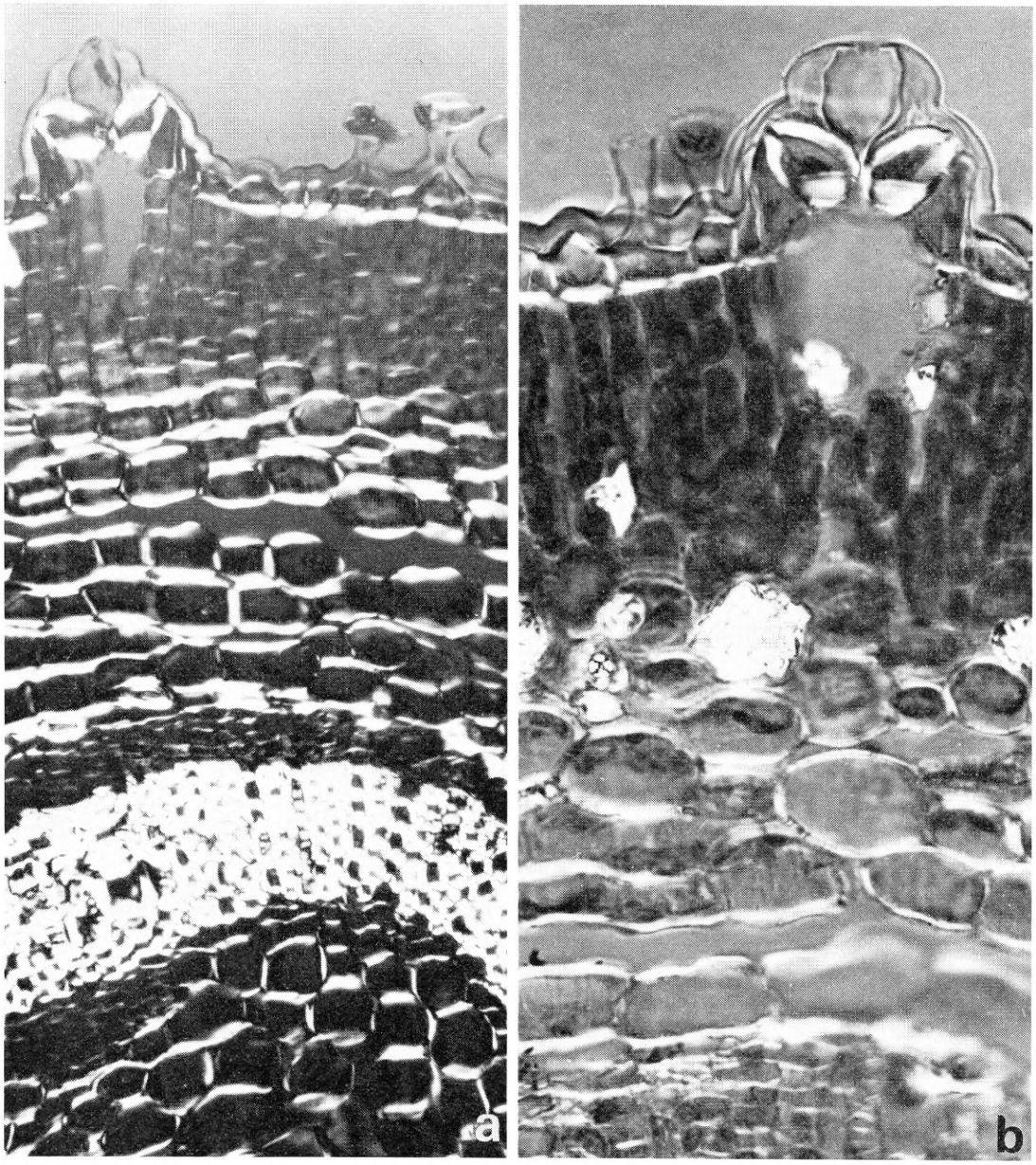


Fig. 26. a. *Fabiana denudata-viscosa* complex, b. *F. imbricata*. Cross sections of stem in semi-polarized light. — In *F. imbricata* crystal druses were abundant in the parenchyma between the palisade tissue and the phloem (below in (b)). In *F. viscosa* the xylem which is very uniform forms a continuous cylinder between the phloem (almost dark) and the pith parenchyma (below), a (× 320), b (× 500).

Occurrence and morphology

Fabiana viscosa is a 0.5–1 m. tall dwarf shrub with virgate stems and branches. It has small leaves but these are shed in the middle of the summer. The young branches are covered with glandular hairs. In older parts the glandular covering is less dense. It is difficult to separate *F. viscosa* from *F. denudata* which is less glandular. These two species grow side by side in Patagonian steppe vegetation in the Atuel valley area, see Böcher, Hjerting & Rahn (1968 pp. 162–163, and 1971), however, their general distribution is different. *F. viscosa* is recorded as southerly as Rio Negro, while *F. denudata* is mentioned by Cabrera (1958) as one of the dominating shrubs in the Provincia Puñeana, which is a montane steppe region in Northern Argentina.

F. imbricata Ruiz. & Pav. is Patagonian and grows in dry woodlands and *Discaria* chaparral distributed from Neuquén to Central Chubut. It is much taller. Pyykkö (1966, p. 509) describes it as a 1–4 m. tall richly branched shrub on which young shoots bear numerous leaves. In the other two species the few leaves disappear soon. They are almost apophyllous, see e.g. Cabrera (1958, fig. 1 b).

Leaf anatomy

The anatomy of the blade of *F. viscosa* was examined by Pyykkö (1966 p. 509) who describes it as centric, 400μ broad and 200–280μ thick with stomata on both surfaces, as well as glandular hairs with long stalks. She further states, that ordinary mechanical tissues are absent, but that the xylem in the vascular bundles probably serves as a supporting system. According to Cabrera (1958) the leaf blades of *F. peckii* are similar, being 277μ thick, although without vascular elements.

Our material (from the Rio Diamante area) deviates somewhat by having some phloem fibers in central vascular bundles, while glandular hairs are missing (Fig. 27 b). The central bundle is surrounded by a sheath of cells which contain chloroplasts. These appear to be smaller than those in the mesophyll, not larger as in most C_4-plants. However, they are situated centrifugally in the sheath cells. The epidermis cells have very thick outer walls which are not cutinized but the walls are covered with a cuticle. They are clearly lamellated and provided with many delicate striae resembling ectodesmata. These do not reach the cuticle. The stomata are not raised above the surface as they are in the stem. Some curious empty airfilled cavities in the thick outer walls are thought to be rudimentary bases of hairs (Fig. 27 d).

A number of transitional stages between some rarely occurring unicellular thick-walled spinous hairs and papillate ± thin-walled hairs were found (Fig. 27 a). One of the papillate hairs had a thick outer wall and an empty cavity below which resembled the cavities in the cells without hairs. The hair cells undobutedly die soon and their lumen becomes airfilled during the preparation.

The leaf of *F. peckii* pictured by Cabrera (1958) clearly belongs to an isolateral type. This may also be the case with the leaf of *F. viscosa* studied by Pyykkö, but in our material the palisade tissue of the adaxial side extends and turns round at the leaf margins thereby framing the green cells of the abaxial side, which, although being

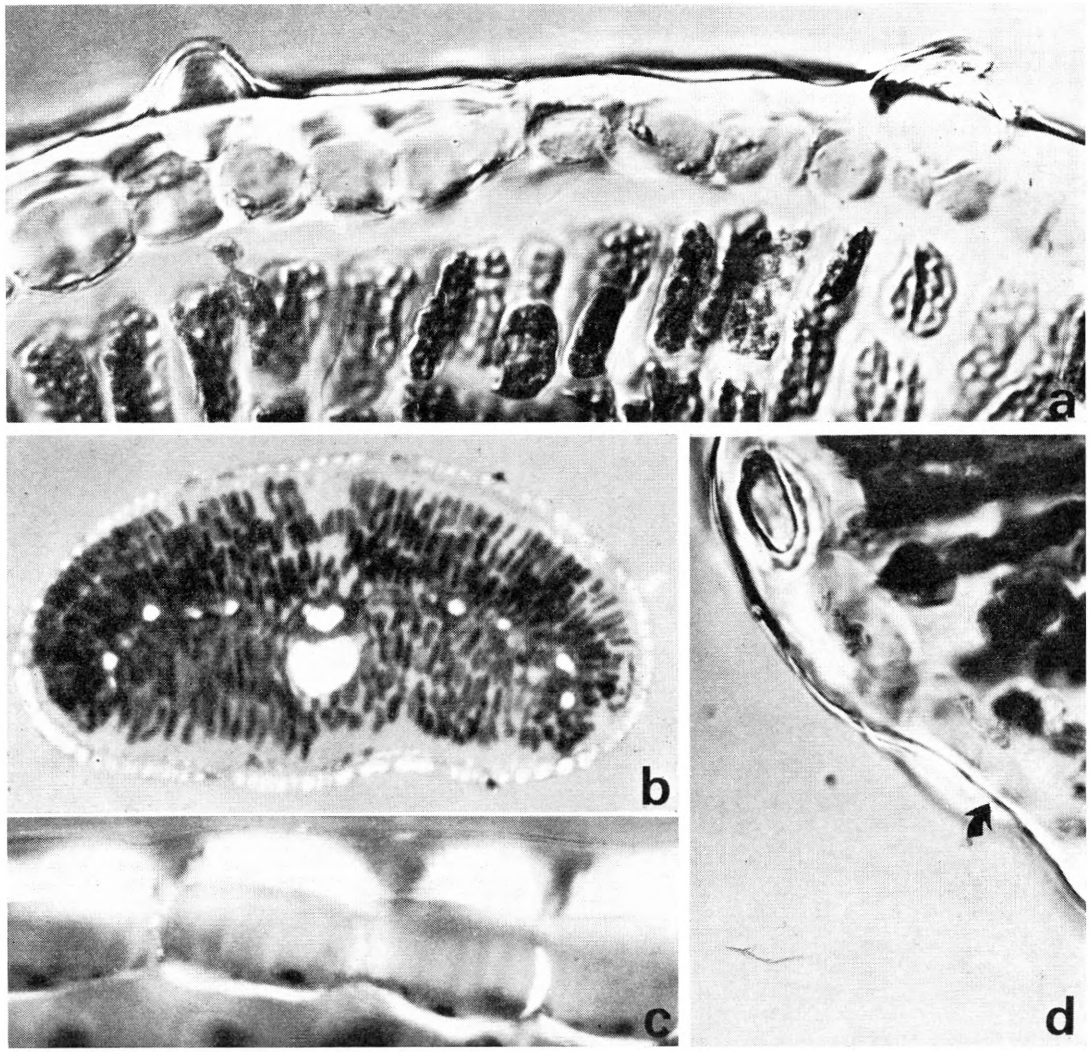


Fig. 27. Leaf anatomy in *Fabiana denudata-viscosa* complex. — a. Epidermis and upper palisade layer; two papillate hairs (interference contrast, × 500). — b. Cross section in polarized light showing position of bundles and the shiny outer epidermis walls (× 80). — c. Epidermis cells with thick birefringent outer walls covered with cuticle (× 640). — d. Part of leaf margin with airfilled cavity in the outer wall of one of the cells and thin-walled area near marginal vein (arrow) (× 500).

elongate, contain less chlorophyll and thus have maintained some of the characters of the dorsiventral type of leaf. In *F. imbricata*, which is less xeromorphic, the leaves according to PYYKKÖ (1966) are angular in transverse sections and dorsiventral.

At the margin of the blade there are also some epidermis cells with thin outer walls (arrow in Fig. 27 d). These are placed outside short green cells radiating from the marginal bundle. Possibly these areas serve as hydathodes.

Scale leaves supporting small buds had some interesting anatomical features. On their backside, or the morphological underside, many cells were decomposed and lignified, in some cases phellem cells were produced. The epidermis on the ventral side facing the bud contained a number of areas with small and low cells with thick lignified porous walls. Towards the surface the lamellate walls were radially striated, the striae being lignified. Many rather wide intercellular spaces were seen in the parenchyma between the vascular bundles and these lignified low epidermis cells. We are most inclined to explain these structures as a kind of hydathodes. Water, perhaps slime, may be liberated from the vascular strands to the intercellular spaces and leave the scale leaves through the low porous cells in the epidermis.

Outline of stem anatomy

Cabrera (1961 p. 236) described the stems of *F. peckii* Niederl. in material from Neuquén, and this description corresponds to that which we are able to put forward about the three species studied by us. In the epidermis the stomata are provided with long front cavities and there are numerous glandular hairs which produce a thick coat of resin which is soluble in strong alcohol. The cortex is divided in an outer zone of green palisade cells and an internal zone of parenchymatous cells without chloroplasts. In young branches the internal cortex is provided with wide intercellular spaces. The conducting tissues are continuous; surrounding the pith there are cylinders of internal phloem, xylem, and an outer phloem cylinder. Phloem fibers are found in a layer which is discontinuous or sometimes absent. In the pith there are usually groups of stone cells. In our material *F. denudata* and *F. imbricata* deviate from *F. viscosa* by a regular contents of crystal druses in the internal cortex cells (Fig. 26b).

Apical meristem

A longisection of a young stem offered the possibility of studying the apical meristem. A group of small meristematic cells is placed on top of a shoot and is separated from the almost fully differentiated tissues in the rest of the shoot by a very narrow transitional area where cells are under differentiation. The meristem is protected by a scale leaf which forms a little cap and at its base has an abscission cork layer. The apical meristem appeared to be dormant, a fact which agrees with the very abrupt transition to the mature tissue.

Epidermis

The outer walls of the normal epidermis cells bulge outwards and are covered with a fairly thick cuticular layer which appears to be continuously lamellated. When using interference contrast the cuticular layer shows a number of layers parallel to the surface. These layers seem not to be interrupted outside the radial walls. The outwards bulging of the cells is easy to see from outside on scanning electron micrographs if alcohol treated material is used (Fig. 29c).

The glandular hairs consist of a wineglass-formed stipe cell and a head which

usually has two cells. The stipe cell is placed on the top of an epidermis cell and a thin wall separates the two cells. The cuticular layer surrounds the stipe cell but becomes thin in the outer part. Some of the smallest heads are formed by one cell only. The common type with two cells separated by a radial wall resembles hairs found in the *Scrophulariaceae*. In a later stage the two cells recede from one another in their distal part and at the same time the free walls get concave. As seen from above the heads become oblong and often bilobate (Fig. 29). Each of the two cells usually contains one small crystal. The secretion collects beneath the cuticle which may be lifted and finally bursts. However, the very irregularly folded surface which is disclosed on SEM pictures (Fig. 29a) indicates that the secretion continues after the first ejaculation or oozing out. The first droplet may exert a pressure which depresses the outer walls in the head. The cuticle may be restored on minor parts of the surface and smaller droplets may then collect and produce smaller folds before the next ejaculation.

Very few glandular hairs have four cells in their heads. In the head (Fig. 30d) there are four concave cells and the remains of a common cuticle.

The many glandular hairs which probably repeatedly can produce a secretion are responsible for the thick sticky resinous cover which is so characteristic of *Fabiana*. On herbarium specimens the sticky material is dried up and irregularly cracked, and the heads of the glandular hairs are difficult to detect (cp. Plate IX). The stomatal openings, however, are seen peeping out, very much resembling rock barnacles (Plate IXb).

The stomatal apparatus in *Fabiana* has a striking appearance due to the conspicuous upright and curving ledges on the guard cells. These ledges issue from the distal side of the outer wall thus being somewhat removed from the stomatal opening.

The ledges from two adjacent guard cells curve in their distal part against one another thus surrounding a fairly big front cavity. The ledges are cutinized, very thick at their bases, and very thin in their distal parts (Fig. 28a). They are built up of very thin layers and traversed by a number of centrally placed, very delicate radiating striae which may be interpreted as a kind of ectodesmata (Plate Xd).

The walls of the guard cells soon get very thick. However, they resemble normal guard cells by having relatively thin walls towards the subsidiary cells and short thin walls outside their narrow parts facing the stomatal pore.

A very peculiar folding of the outer walls was particularly easy to observe by using interference contrast or polarizing microscope (Fig. 28a and Plate Xb, c). The folds became numerous outside the narrow parts of the protoplasts and in the walls facing the substomatal chamber. Of importance for the interpretation of these folds may be the fact that they are formed in the outer parts of the wall where this gets particularly thick, and that the microtome knife is able to tear off the cuticle which has covered the wall (Plate Xb, leftmost guard cell). If we assume that the increase in wall thickness is connected partly with a withdrawal of the protoplast, partly with an increase in cell size, the latter growth might involve tensions in the outer wall which would then create the folds and perhaps loosen the cuticle. On the other hand

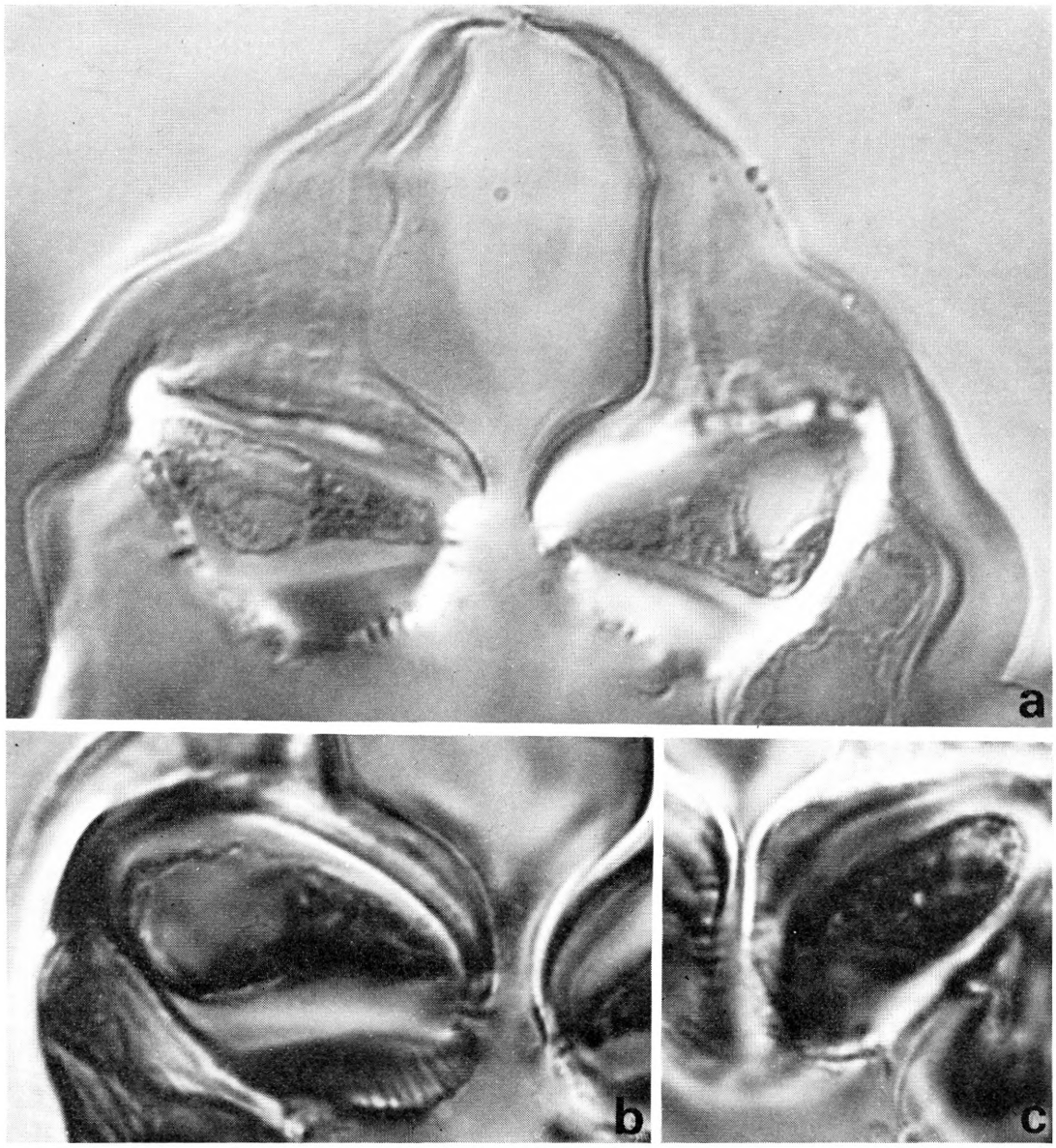


Fig. 28. Stomatal apparatus in *Fabiana denudata-viscosa* complex. — a. Interference contrast. — b–c. Semi-polarized light (× 2000).

such folds may contribute to make the thick walls less stiff and thus be of physiological importance.

The thin wall sectors towards the subsidiary cells deviate from other stomatal complexes by being relatively short. They only constitute the inner half of the wall

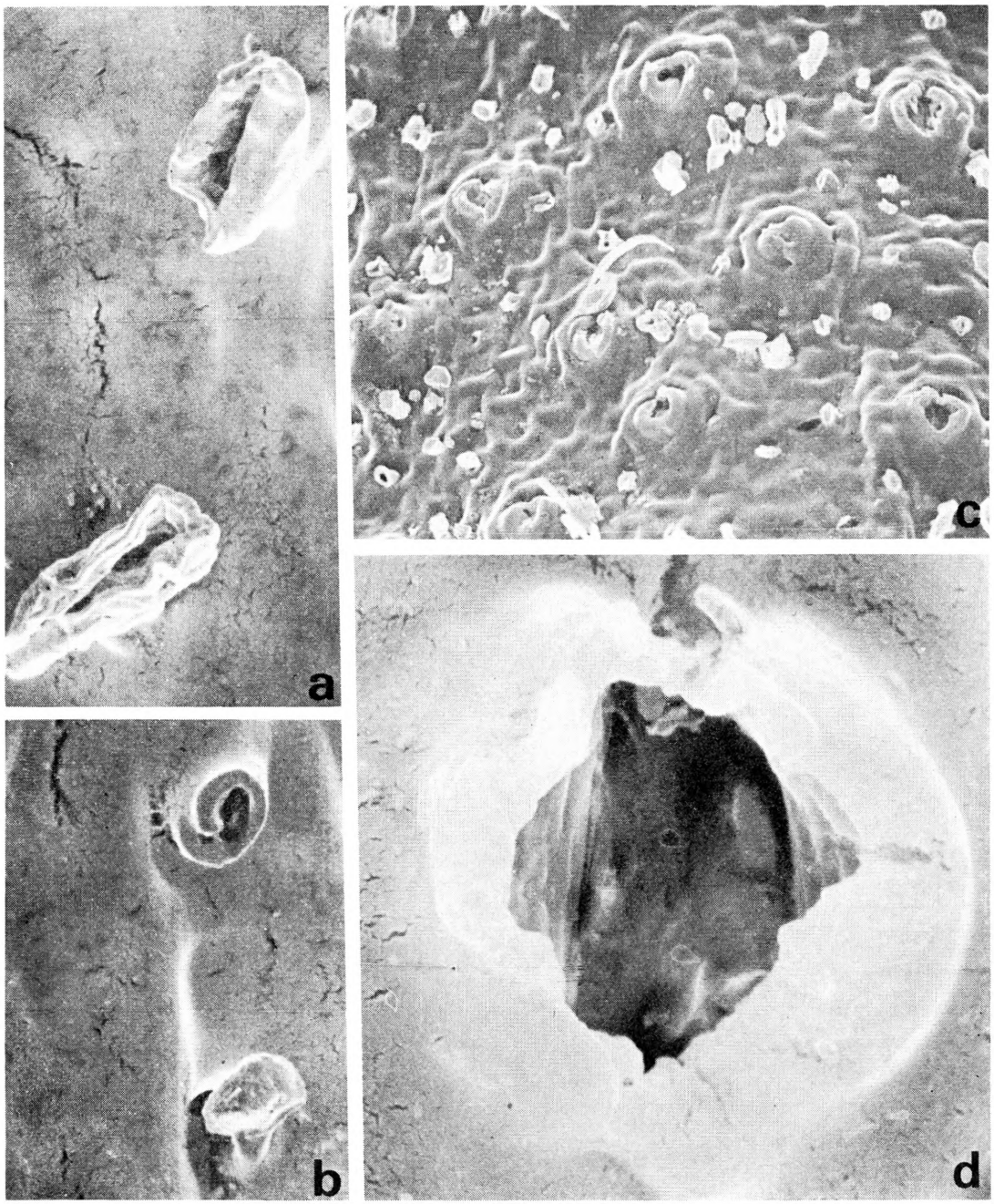


Fig. 29. SEM micrographs of stem surface in *Fabiana denudata-viscosa* complex after treatment with alcohol (cp. Plate IX for untreated material). — a–b. Glandular hairs and hair base (× 950). — c. Stomata and glandular hairs (× 200). — d. Stomatal opening, note foldings in walls on both sides of front cavity, cp. Fig. 28 (× 2000).

distal to the pore. In a turgescent stage a bulging of the thin sector will not only open the pore but probably also pull the ledge so that the entrance to the front cavity opens up more. An outwards movement of the ledges will probably involve a pull by which the folds may act as the folds of an accordion. By strong movements and wide openings of the entrance some of the folds may be visible when observed from outside (Fig. 29 d).

The peculiar stomatal apparatus in *Fabiana* resembles that of *Monttea aphylla* which was described in our previous paper (Böcher & Lyshede 1968 Plate I, III d and VIII b–f). *Monttea* belongs to a closely related family (*Scrophulariaceae*).

Ontogeny of stomatal apparatus. Longisections of the epidermis from a point near the stem apex are shown in Fig. 30 a–b. The initials of the guard cells are larger, elongate cells with outwards bulging outer walls. Almost immediately the outwards bulging parts appear translucent and are clearly developing into the front cavity. The subsidiary cells curve outwards thereby producing a substomatal chamber.

Lenticels

Lenticels are usually limited parts of a periderm. In the younger parts of the *Fabiana* stems such structures occur in a unique way being surrounded by green cortex cells or even parenchyma cells in deeper lying areas of the stem.

As in normal periderm lenticels the deviating type is initiated and develops below a stoma. As it appears from Fig. 31 b the substomatal chamber is first filled with large suberized cells. In contrast to normal lenticels no phellogen is formed, but the suberized cells increase in number. The lenticel enlarges in breadth at the same time as it grows inwards between the green outer cortex cells. During this growth the suberized cells produce intercellular spaces which seem to be formed partly schizogenous and partly by decomposition of some of the cells.

The suberized cells form more or less cylindrical areas reaching the inner cortex parenchyma or may in some cases continue through somewhat necrotic looking openings in the cylinder of vascular tissues into the pith parenchyma.

The lenticels in *Fabiana* are believed to make gaseous exchange more easy. If the stomata close during unfavourable conditions the lenticels will enable oxygen to penetrate to the living cells in the interior of the stem. During the respiration carbon-dioxide will be formed and may reach the green cells from below. It is worth mentioning that the lenticels were found only in areas where the density of secreting glands was highest. Young shoots are completely coated with the sticky secretions from the glands and this may make it particularly difficult for the deeper lying cells to get enough oxygen.

Cortex

Stem transections of all three species show a clear difference between an outer cortex tissue with green radially stretched cells and few or no crystal druses and an inner parenchymatous part which in our material of *F. denudata* and *F. imbricata* has many druses.

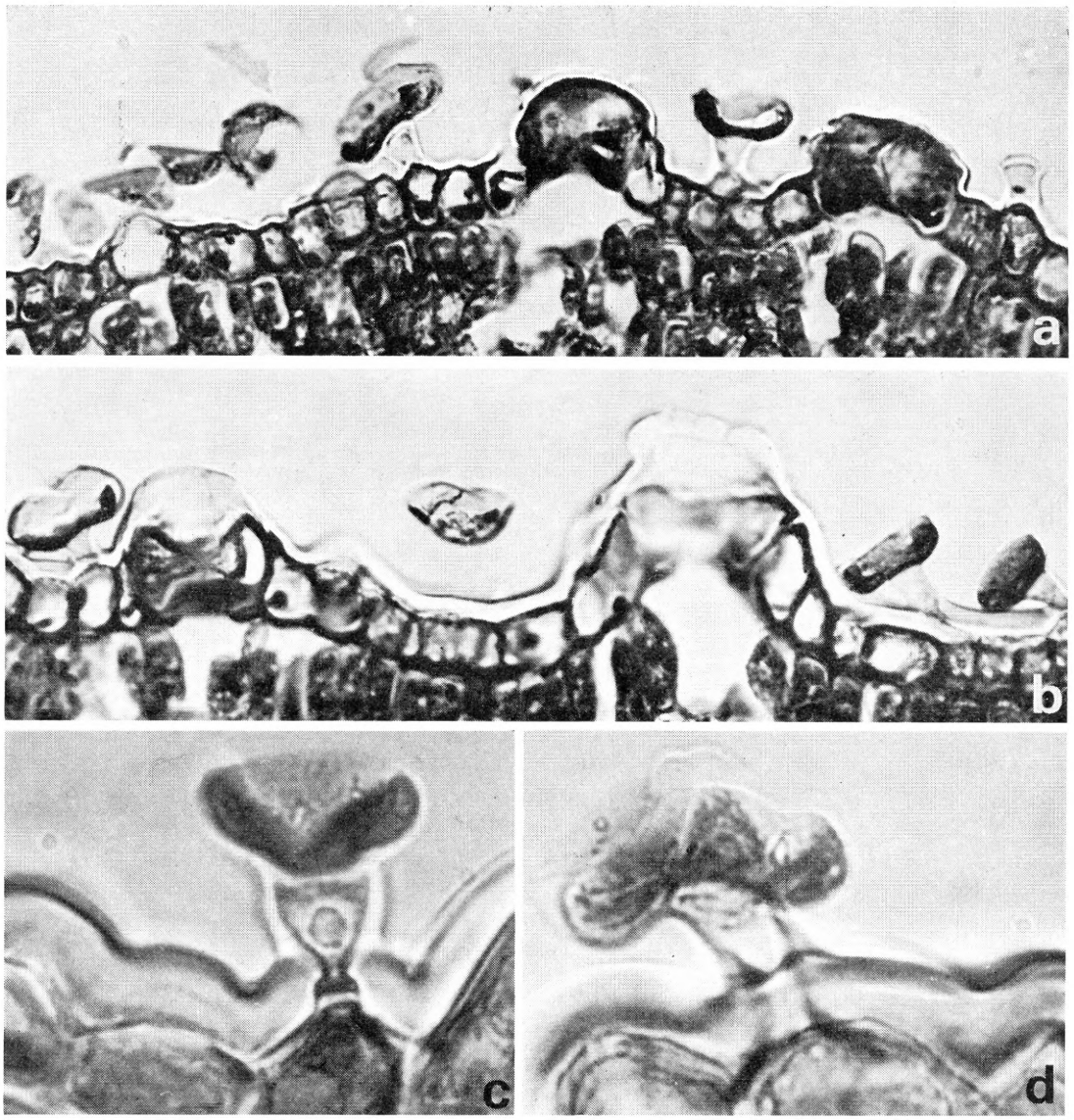


Fig. 30. *Fabiana denudata-viscosa* complex. — a–b. Development of stomata in young stem (× 500). — c–d. Glandular hairs and outer epidermal walls (× 1280).

Stele

The abaxial side of the outer phloem cylinder is frequently accompanied by a layer of fiber cells. This layer is not continuous making the exchange of substances between the photosynthetic cells and the conducting tissues possible.

In older stems of *F. imbricata* the secondary phloem is stratified by the occur-

rence of cylinders of sclerenchymatous cells. These cylinders, however, are never continuous. In longisections the sclerenchymatous cells are elongate and form radial rows.

The continuous xylem has many protoxylem rows, but these are uniformly distributed and do not suggest the occurrence of primary vascular bundles in the young stem. The protoxylem borders a cylinder of internal phloem. In our material of *F. viscosa* the xylem is very uniform with many uniseriate rays and narrow mostly uni- to biseriate areas with fibers and tracheary elements. No wide vessels were observed in normal wood of *F. viscosa*, but very wide elements were formed in certain areas in the stem which for some reason had anomalous structure, e.g. with a number of dying or decomposed cells. These areas were believed to have connection to or be part of the curious lenticel system mentioned above. Annual rings in the wood are not conspicuous. In the wood of *F. imbricata* scattered wide vessels occur, but also here the annual rings are indistinct.

Frequently the pith contains cells with very thick secondary walls. In longisections groups of stone cells form irregular more or less curved rows. In such groups e.g. of four cells the terminal cells frequently taper suggesting fusiform initials for such groups.

3. Species in which the cortex chlorenchyma is more or less interrupted by fiber strands reaching the peripheral layers.

This group has clearly an intermediate position between the first group with terete stems and no clear ribs or furrows, and the furrowed type (p. 96). In most species the stems are ribbed and the ribs are supported by fibrous strands which as a rule are perivascular and in several cases situated inside an endodermis which bulges out inside the ribs. Stomata are usually placed between the ribs and outside a section of the cortex chlorenchyma.

Psila spartioides (Hook. & Arn.) Cabr. (Asteraceae)

Material: W. Argentina, Mendoza Prov., Atuel valley area, east of Estancia El Sosneado. Böcher, Hjerting & Rahn No. 2086, Jan. 4, 1956.

Occurrence and morphology

Psila spartioides is widespread in the salt steppes of W. Argentina. It was collected in the provinces of Mendoza and Neuquén at several stations, mostly in depressions near salt lakes e.g. dominating together with *Distichlis scoparia, Heterostachys ritteriana, Atriplex lampa, A. boecheri, Sporobolus rigens,* and *Chuquiraga erinacea.* These areas were in all cases surrounded by dry vegetation classified as Patagonian steppe (Böcher, Hjerting & Rahn 1972). In Chile *Psila spartioides* occurs in saline coastal dunes formed around *Salicornia peruviana* (Kohler 1970 p. 122).

Psila spartioides and *P. retamoides* which will be mentioned later are both almost leafless. From the Puña vegetation Cabrera (1958) mentions *P. boliviensis* which has

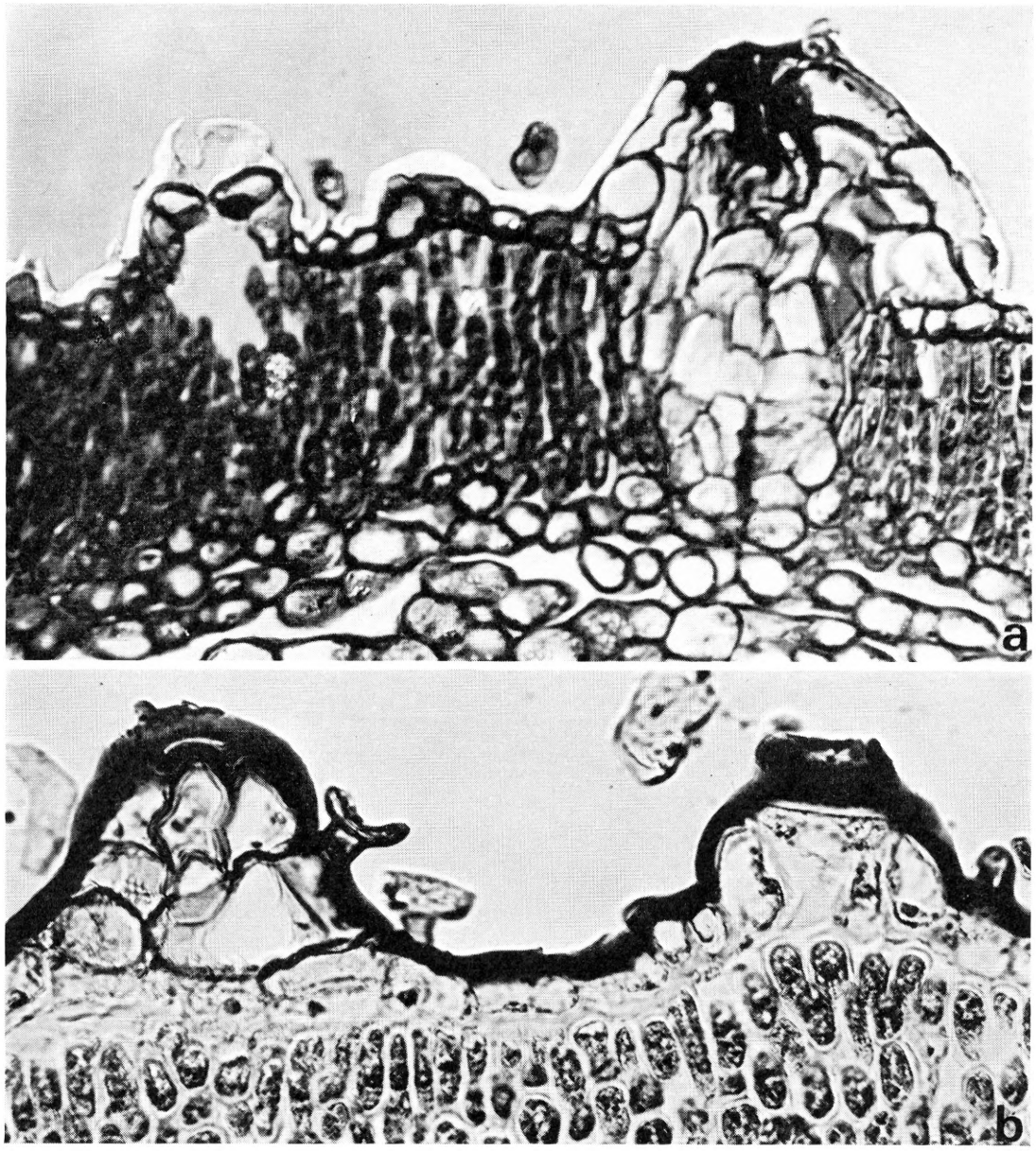


Fig. 31. *Fabiana denudata-viscosa* complex showing development of lenticels in young stems, initial stage in (b) on the left. — a. Quadruple staining and interference contrast (× 320). — b. Sudan IV staining (× 500).

many small leaves, but this species also has a var. *latifolia*, a fact showing that a reductional series regarding leaf size and number of leaves exists within the genus.

Psila spartioides is a branched dwarf shrub with fascicled branches. The stems

appear somewhat angled and glabrous. However, glandular hairs are abundant in young branches but they degenerate early except for their cutinized basal cells. The few scattered leaves are about 1 cm long, 1 mm broad, somewhat succulent, and carry a few marginal hairs. Resinous masses are secreted in the axils of leaves and scale leaves. The anatomy of the scale leaves will be mentioned in connection with the outline of stem anatomy.

Outline of stem anatomy

The epidermis is described below. The stems in our material may be enneagonal but with no sharp ridges. The blunt corners are supported by 2–3 layers of collenchyma and by strong fiber strands which, however, are separated from the collenchyma by the endodermis. The walls of the endodermis cells are suberized (see Fig. 32a). Between two ridges one large duct occurs. The suberized cells which line the duct as an epithelium are connected with the suberized endodermal cells. Behind the ducts there is usually one fiber strand which in cross sections appears ± triangular (Fig. 32a). Longisections of the stem show that the ducts do not run continuously through the internodes. They appear as a series of big cavities which are linked together by diaphragms of thin-walled cells which may be dissolved at a later stage so that a continuous system of cavities develops (cp. Fig. 34c).

In cross sections the vascular tissues have a stellate outline. Inside the ridges and the outermost fiber strands the phloem and xylem radiate, while they bulge inwards behind the ducts. Here the phloem occupies particularly broad areas. An exchange of substances between the green cells and the conducting tissues is secured by a number of non-suberized passage cells in the endodermis between the ducts and the corner fiber strands (* in Fig. 32a).

The scale leaves have a few green cells on both sides. In the middle they are traversed by a vascular bundle which on the abaxial side is accompanied by a duct. Sometimes the bundle terminates below the tip of the scale where the broad tracheids are succeeded by parenchymatous cells probably acting as an epithem. The groups of broad tracheid cells may serve as a water storage area. The tip itself has several stomatal pores or large openings resulting from decomposition of epidermal cells. We assume that water at an early stage is secreted directly from the tracheids or from the parenchyma, while resinous substances may be liberated later from the ducts through the openings at the tip. The fact is that resinous masses are found in connection with scale leaf margins. Near the bases of the scale leaves abscission cork is formed.

Epidermis

The epidermis in *Psila spartioides* is of particular interest because of the striking structure of the stomata and the trichomes. Another interesting feature is the cutinization of the inner walls of the cells. From observations in SEM it appears that the stomatal openings are provided with very large almost vesicular front cavities. On the outside the front cavities have oval openings and are surrounded by a groove. The

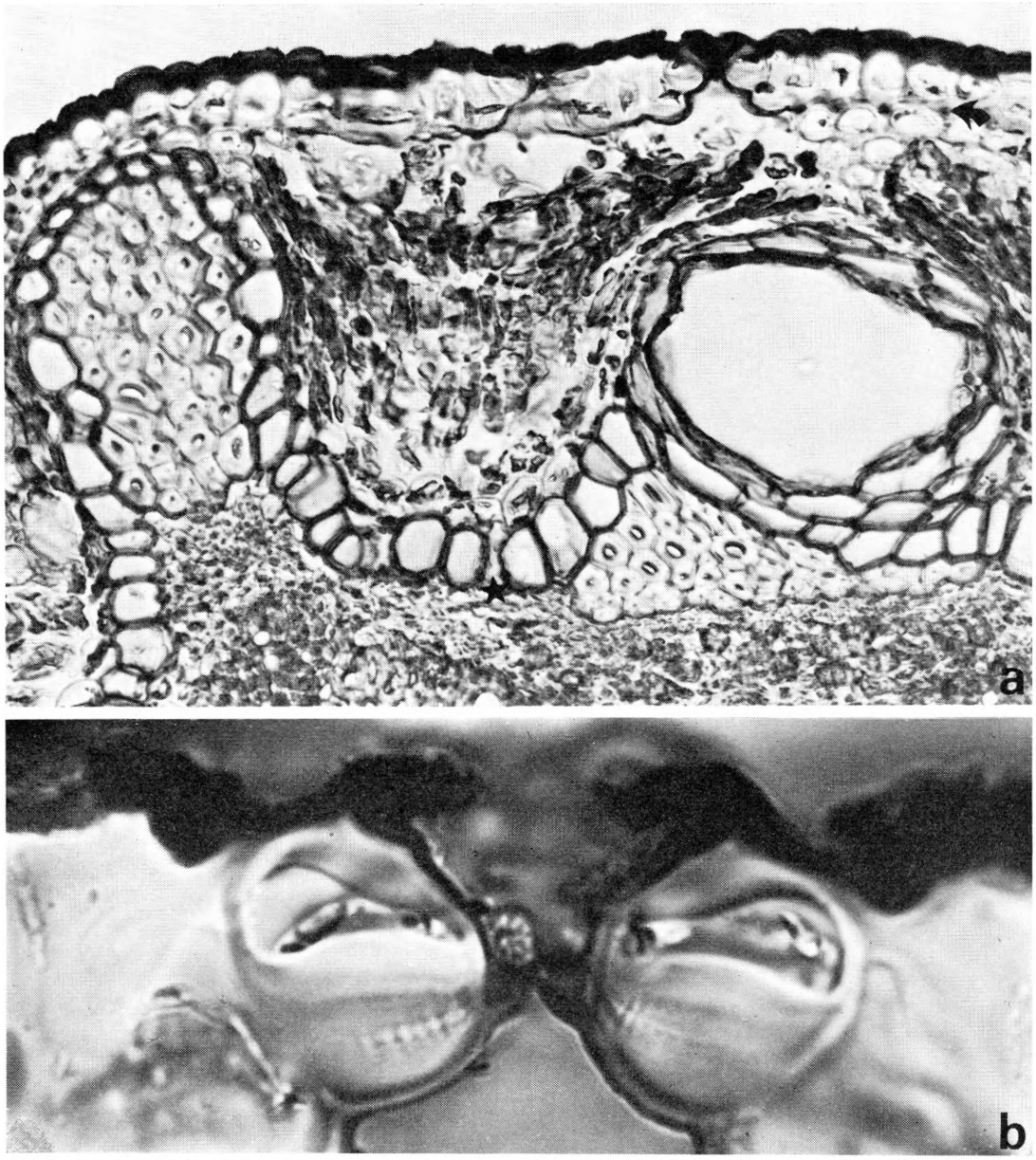


Fig. 32. *Psila spartioides*. a. Cross section of stem. Sudan IV stains thick cuticular layer in outer epidermal walls as well as walls bordering substomatal chambers and sections of walls separating epidermis and hypodermis (arrow). Endodermal walls are also stained except in passage cells (*). The endodermis surrounds phloem fiber strands and borders wide lysigenous cavity which is lined by suberized cells. Photosynthetic cortex between two endodermal bulges (× 320). — b. Cross section of stomatal pore, Sudan IV staining. There are three cutinized ledges; an outer ledge delimiting the front cavity, an interior one, almost closing the pore, resembling two opposite beaks, and a median very small one near narrow parts of protoplasts. Thick interior walls of guard cells lamellated and traversed by micro-channels (semi-polarized light, × 2000).

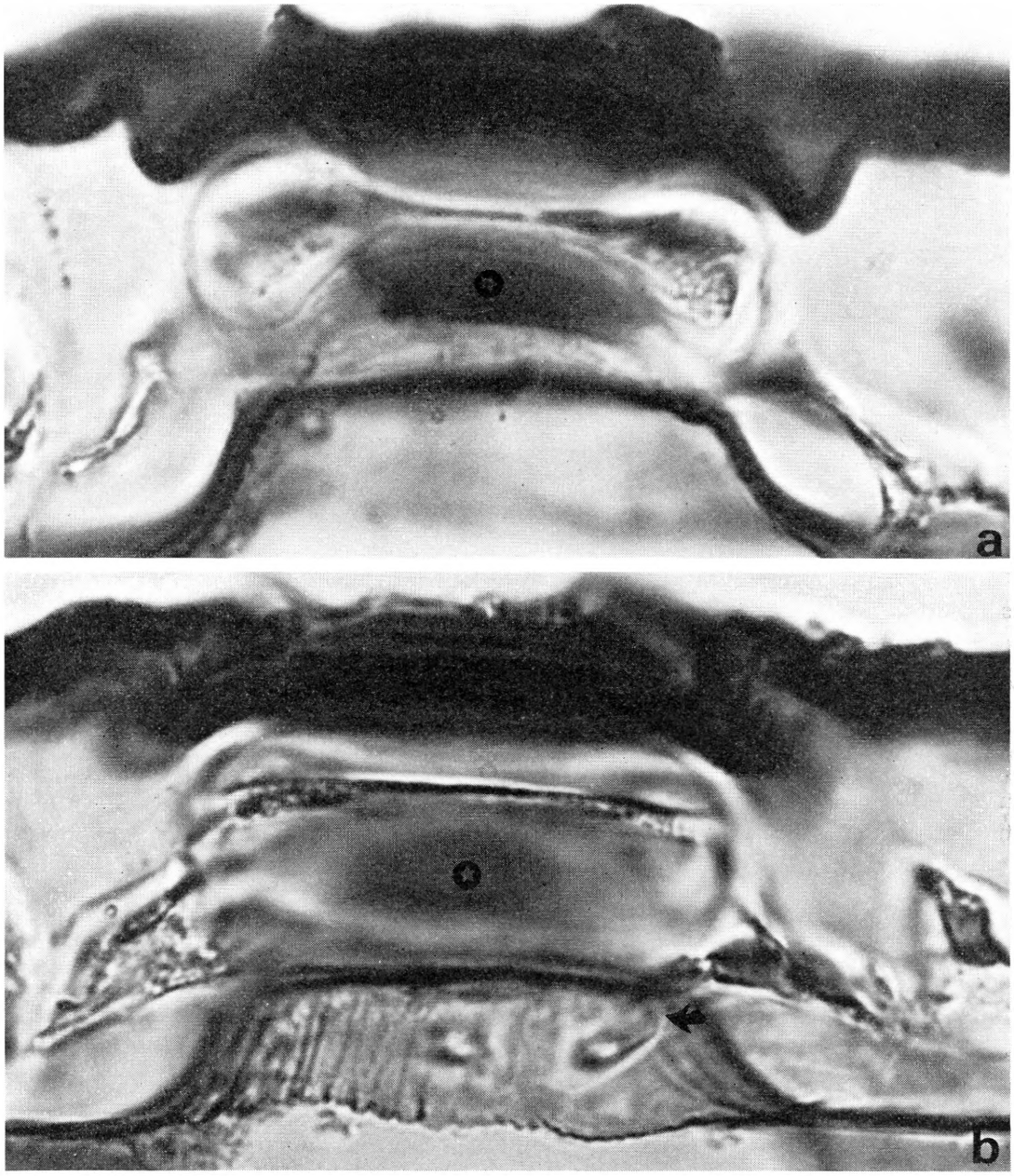


Fig. 33. *Psila spartioides*. Longitudinal view of guard cells stained with Sudan IV. — a. Close to central pore. — b. Low focal plane showing furrowed wall of subsidiary cell towards substomatal chamber. Dark oblong area in the center (*) is due to the interior cutinized ledge (see Fig. 32b), dark line below indicates the corner where the guard cell adjoins the subsidiary cell. At arrow, plasmatic connection between subsidiary cell and cell on the right side of the guard cell. Outside bulbous ends of guard cells, in (a) a deep furrow probably functioning as a hinge (× 2000).

vesicular protruding front cavities result from a peculiar modification of the outer ledges issuing from the outer thick walls of the guard cells. The inner thick walls, however, are also provided with strong ledges which like two sharp wedges almost close the passage from the front cavities to the substomatal chambers (Fig. 32b, Plate XIId).

The outer and inner ledges are cutinized as are the outer walls towards the front cavity and the substomatal chamber. The cuticular surface, however, is covered by wax deposits which crack (Plate XI). Some of the wax scales bridge the grooves around the vesicular front cavities as well as the small grooves outside the radial walls in the epidermis. By treatment with alcohol this wax pattern disappears, while a number of cracks in the cuticular surface corresponding to the many incissions which may be seen in cross sections of the cuticular layer become visible (Plate XII). From the cell lumina of the guard cells micro-channels or minute cavities extend into outer ledges. The thick inner walls are lamellated but are further radially striated (furrowed). The walls of the subsidiary cells towards the substomatal chamber are also remarkably furrowed (Fig. 33b). In many respects the stomatal structure in *Psila spartioides* resembles that already described in *Fabiana* (p. 54). In both cases the subsidiary cells are placed obliquely downwards in relation to the bulbous backside of the guard cells. From Plate XIIa–b it appears that the opening to the front cavity varies much sometimes being narrowed to a fissure. The opening movement presupposes forces directed obliquely downwards. The furrows in the interior walls of the guard cells and in the walls of the subsidiary cells towards the substomatal chamber may facilitate the movements, and the groove which surrounds the front cavity may act as a hinge.

Psila spartioides appears glabrous, but on the surface there are many remains of trichomes in the form of cutinized basal cells belonging to glandular or non-glandular trichomes. Branch primordia which in this species may be found in a dormant condition in the axils of scale leaves seem to be entirely embedded in resinous masses. In alcohol material these substances are removed and the stems and leaves of the small primordia are found to be densely covered by various trichomes. The dominant type is a glandular trichome which above the cutinized basal cells consists of a row of 2–4 secretory cells which upwards increase in size. We have seen oil droplets in some of these cells but in by far the most cases the cells were empty and shrivelled. Many cells had marginal cuticle folds resembling those described by KLUG (1926) in glands of *Mentha piperita*, while some of the trichomes had only one large peripheral cell with some cuticle folds. The glandular hairs in *Psila* clearly resemble the uni- or biseriate multicellular glands found in other members of the *Asterales* thus in *Parastrephia*, where leaves and stems are extremely resinous due to the activity of such glands (SOLBRIG 1961 p. 278 and fig. 20–21). However, the glandular hairs found on the dorsal side of the leaves in *Cassiope tetragona* also have a similar structure (H. E. PETERSEN 1908).

Another less common type may be described as peltate glands. They consist of a few-celled stipe and 1–3 layers of cells in the glandular head.

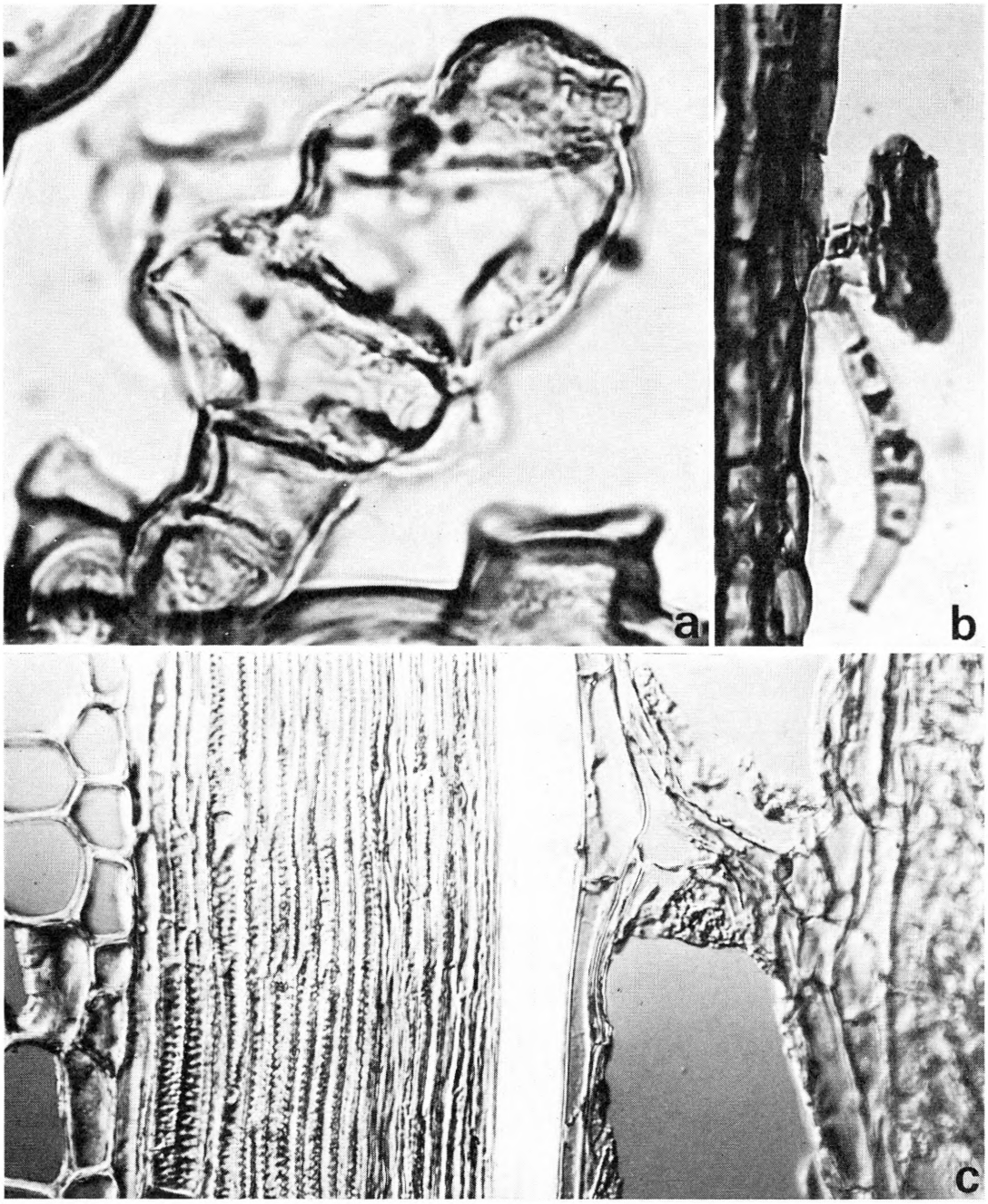


Fig. 34. *Psila spartioides*. a. Empty glandular trichome, its two basal cells cutinized; on the right one such basal cell left while excreting part of trichome has disappeared (Sudan IV staining, × 2000). — b. Cluster of peltate gland and mucilaginous hair (× 500). — c. Longisection of stem from the left showing pith parenchyma, xylem, phloem, phloem fibers, diaphragm between two cavities and green cortex (interference contrast, × 320).

A third type is built as one row of rather short cells with cutinized walls carrying one or a few elongate cells which are rich in cytoplasma. In these terminal cells the cell walls decompose and seem to be transformed into mucilage. In a few cases the hairs were neither glandular nor mucilaginous, but just a row of cells.

A characteristic feature is the frequent arrangement of the trichomes in small clusters. 2–4 cutinized basal cells are placed close together. The cluster may consist of 2–3 hairs of the dominant glandular type, or one such and two mucilaginous ones. The combination of one peltate gland and one mucilaginous hair was also observed (see Fig. 34b).

Psila retamoides (Phil.) Cabr. (Asteraceae)

Material: W. Argentina, Mendoza Prov., 25–30 km north of Mendoza. Böcher, Hjerting & Rahn No. 2099, Jan. 6, 1956.

Occurrence and morphology

The material of *Psila retamoides* was collected in subtropical shrub steppe (Monte-vegetation) near a dried up river together with *Proustia ilicifolia*. It was further observed in a very scattered vegetation of *Larrea nitida* and *Opuntia* at a point 204–205 km north of Mendoza. Also *Bulnesia retama* (Part I pp. 21–29), *Cercidium australe*, and *Atriplex lampa* were noticed in the same community. The occurrence of both *Proustia* and *Larrea nitida* indicates that the soil in which *Psila retamoides* grows is moderately dry.

These observations agree with the results published by Roig & Roig (1969), who state that *Psila retamoides* is a characteristic element in the *Bulnesia* zone along the foothills of the Precordillera. While *Bulnesia* dominates more sandy areas, *Psila retamoides* is abundant in stony dry river beds. Roig publishes three analyses of the *Psila retamoides*-community which contains species such as *Eupatorium patens*, *Senecio gillesianum*, *Wedeliella incarnata*, and *Baccharis salicifolia*.

P. retamoides is leafless, but has very small scale leaves (Fig. 36c). The surface is sticky and almost completely covered by a resinous substance, which gathers in great masses in the axils of branches. Under the resinous cover the surface is papillate. No trichomes are seen, but in the same way as in *P. spartioides*, small axillary shoot primordia are densely covered by trichomes. On the surface of older stems only the cutinized basal cells of trichomes are left.

Outline of stem anatomy

The stem structure of *P. retamoides* strongly resembles that of *P. spartioides*. The stems may be octagonal. The ribs are blunt. Below the papillate epidermis 2–3 rows of collenchyma are found outside the fiber strands. The latter surrounds a duct and is traversed by the suberized endodermis (Fig. 35) which is composed of smaller cells than in *P. spartioides*. Triangular fiber strands are found behind somewhat larger ducts halfway between the ribs. Occasionally the fiber triangles expand tangentially and

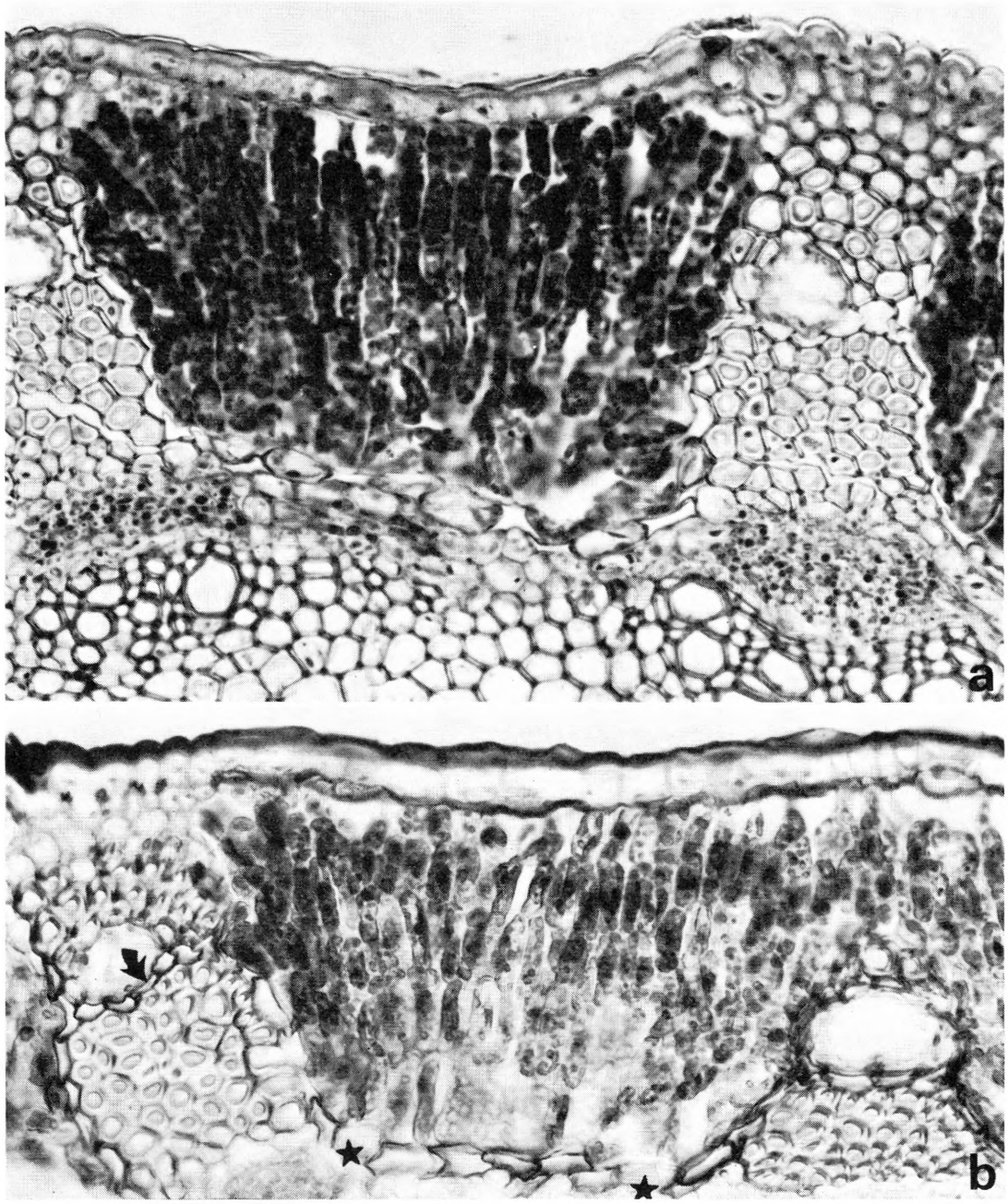


Fig. 35. *Psila retamoides*. a–b. Cross sections of stem, in (b) treated with Sudan IV which stains outer and inner walls of epidermis as well as endodermis except passage cells (e.g. at ★). Endodermis cuts left-hand fiber strand inside secretory duct (arrow) and surrounds larger duct on the right (× 320).

cover fairly broad phloem areas. Inside the corner fiber strands the phloem strands are usually small. Sometimes the larger ducts are on their abaxial side provided with a few fiber cells. The endodermis has many passage cells inside the areas of green cortex palisade cells (* in Fig. 35). Phloem and xylem first occur in vascular bundles inside phloem fibers. Later a continuous cambium and a complete cylinder of secondary vascular tissues are formed. Sometimes the mechanical tissues in the corners expand tangentially and may contain a row of three ducts. The endodermis reaches the interior sides of these ducts but is interrupted as a result of the expansion (Fig. 36 d). Phellogens are sometimes formed below the corner fiber strands which are finally thrown off together with the living primary tissues.

In one case all the tissues outside the endodermis and between two corner fiber strands had been shed. Obviously the lignified fibers and the suberized endodermis gave sufficient protection to the tissues inside the wound.

Epidermis

While the trichomes appear to be very similar to those found in *P. spartioides*, there are obvious differences between the two species with regard to the stomata and the surface appearance. On SEM pictures (Plate XIII) at low magnification the areas between the ribs have numerous depressions in which the stomata are found. They are orientated in many directions, and the outer ledges are not forming vesicular front cavities as they do in *P. spartioides*. In addition to the stomatal depressions numerous basal cells of trichomes form clusters which resemble small irregular warts (Plate XIII a). The stomata are much simpler and smaller than in *P. spartioides*. In cross sections the outer cutinized ledges of the guard cells resemble the beak of a parrot. There are no inner ledges, but the walls of the subsidiary cells facing the substomatal chamber are furrowed as in *P. spartioides* (Fig. 36 b). As in that species the inner walls of the epidermal cells are cutinized almost all the way around the stem (Fig. 35 b).

The trichomes are clustered and each little group may contain up to four trichomes which resemble the dominant hair type in *P. spartioides*, but are smaller. Most of the cells are empty, but in very young hairs the cells are filled with a dark substance. In some hairs the distal cells are mucilaginous. In a few cases a beaked structure was observed which might be interpreted as a place through which the secretion had been released.

Prosopidastrum globosum (Gill. ex Hook. & Arn.) Burkart (Mimosaceae)

Synonym: Prosopis globosa Gill. ex Hook. & Arn.

Material: W. Argentina, Mendoza Prov. from area north of Uspallata, 2050 m. above sea level. Böcher, Hjerting & Rahn No. 2212, Jan. 8, 1956, and Estancia El Sosneado, Atuel river area, 1600 m. above sea level. Böcher, Hjerting & Rahn No. 1393, Dec. 3, 1955.

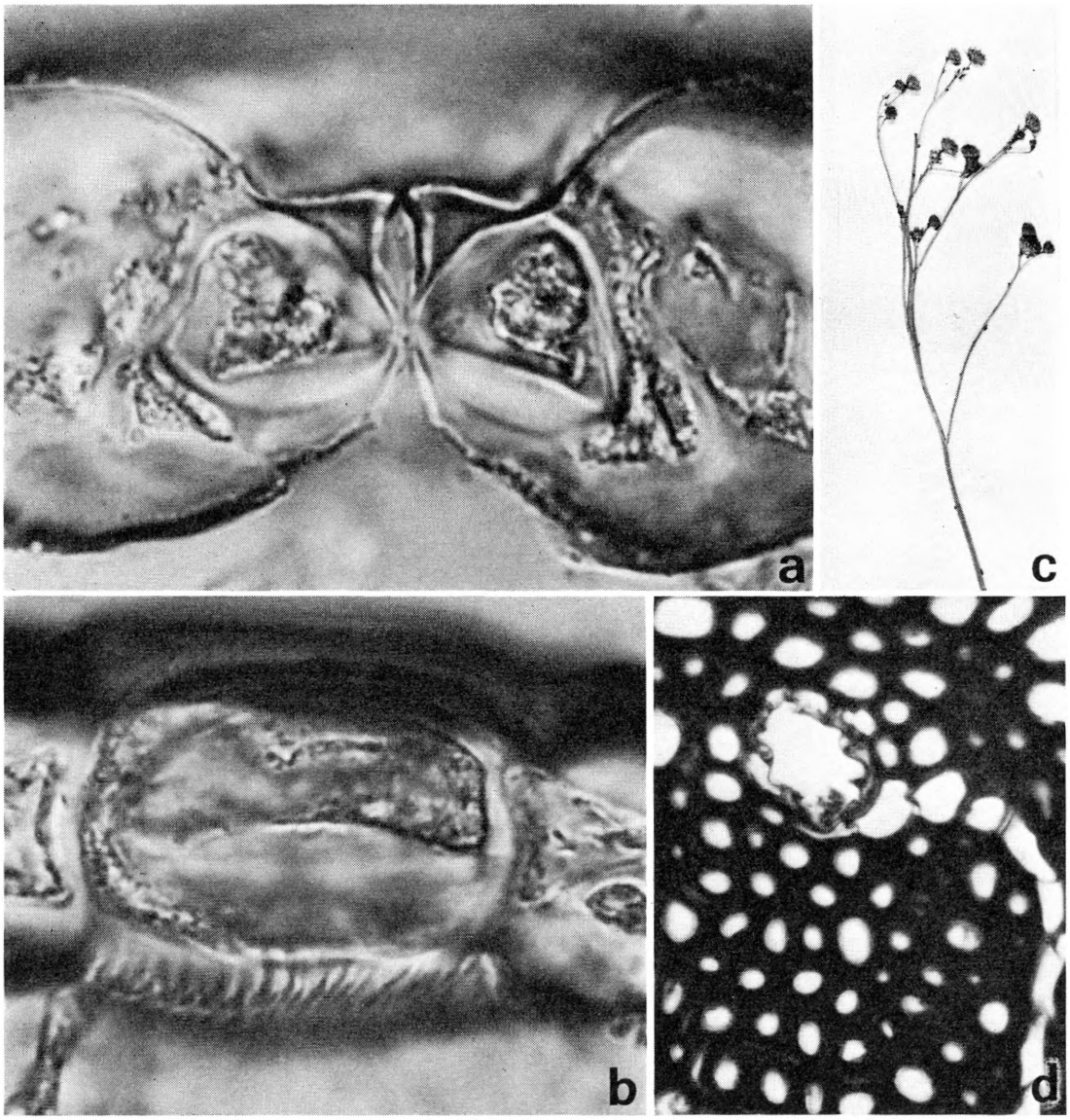


Fig. 36. *Psila retamoides*. a–b. Cross section and longitudinal view of guard cells, in (b) furrowed wall of subsidiary cell distinct (× 2000). — c. Upper part of plant (× 1/3). — d. Endodermis traversing broad fiber area inside rib and contacting secretory duct (Quadruple stain, × 500).

Occurrence and morphology

An 0.3-2 m. tall shrub distributed in the subtropical shrub steppe in the Argentinian Monte-province. Abundant in many places in the lower part of the Atuel valley where it ascends to 1800 m. above sea level. Found mostly in sandy soil, see BÖCHER, HJERTING

& RAHN 1972 (as *Prosopis globosa*). In Monte-vegetation north of Uspallata *P. globosum* was abundant in a *Larrea divaricata* sociation together with two other apophyllous species viz. *Cassia aphylla* and *Fabiana denudata*. The vegetation also comprised species like *Pappophorum sacchariodes* and *Argylia uspallatensis*. Our material consists of young twigs, only about 2–4 mm in diameter, and according to the number of growth rings, 1–2 years old. The twigs are angled, polygonal in cross sections. The corners stand out as low ribs (see ROIG 1970, Plate 50 fig. 5).

The small leaves are basically bipinnate but are often reduced and appear simple pinnate with one pair of leaflets on both sides of the rhacis which terminates in a mucro (ROIG, l.c. fig. 6). Larger bipinnate leaves have two opposite divisions each with as many as 8 leaflets, however, frequently consisting of one large terminal leaflet and 1–3 smaller ones below. At the base two stipules occur which develop into thorns. The leaflets, petioles, and young stems have scattered hairs, in contrast to the pedicels which are densely hairy. Along the margins of the leaflets and on their surfaces as well as at various points on stems and petioles gumlike substances are exuded to form small often hemispherical, sticky and yellowish "tears".

Leaf anatomy

The leaflets are isolateral usually with two layers of palisade tissue on both sides of the vascular strands. An approaching to dorsiventral structure occurs where the adaxial side becomes more vigorously developed. The epidermal cells are usually big and the outer walls covered by a cuticle. Inner walls near stomata also have a cuticle. The stomata become sunken because the small guard cells are inserted between swollen epidermal cells. The guard cells have small outer ledges.

A very interesting feature is the occurrence of epidermal areas where all or most cells appear collapsed, flattened and with dark contents. Evidently it is mainly the anticlinal walls which are decomposed, while parts of the outer and inner walls are maintained. The cuticle is intact and unaffected. The cells are clearly dead. Guard cells occurring together with the collapsed cells remain normal looking because of their thick resistant outer and inner walls. The green cells border on the collapsed epidermis cells and may exert the pressure which led to the flattening. In two cases which are illustrated in Fig. 37 gum masses were found just outside the areas with collapsed cells. In Fig. 37 c the gum mass occurred near a stomatal pore, while in Fig. 37 a such a pore could not be demonstrated. Instead a narrow pore was observed in the outer wall of one of the flattened cells. It was filled with the dark-coloured substance and continued in a funnel-shaped area reaching the gum-deposit outside (Fig. 37 a upper corner on the right). The latter was granulated on the surface and was possibly near its margin covered by remains of the cuticle. We assume that *P. globosum* as is the case with species of *Acacia* by decomposing cell walls can produce gums. The exudation of gums in *Prosopidastrum* seems to take place through stomatal pores or pores found in the partly decomposed outer wall.

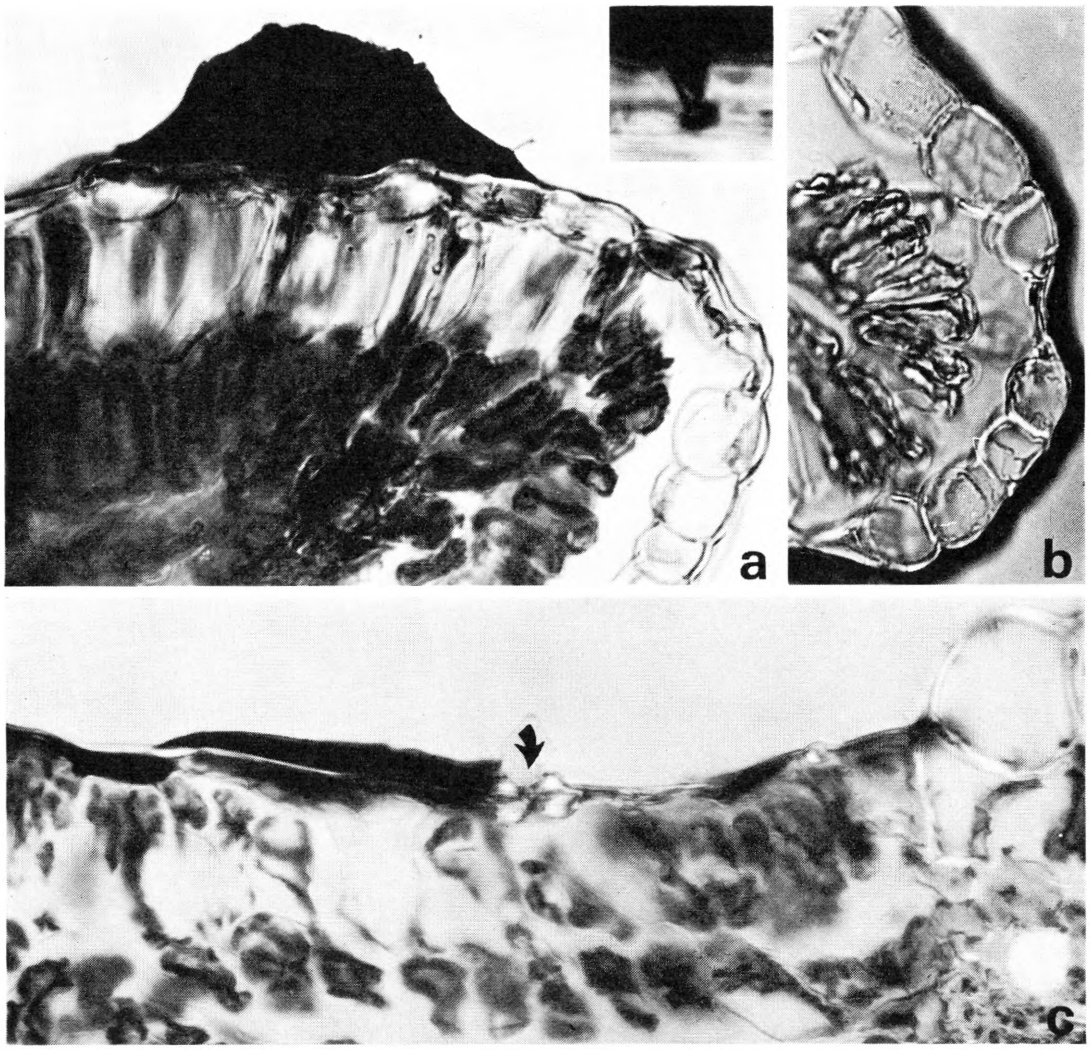


Fig. 37. *Prosopidastrum globosum*. Leaf anatomy. — a. Margin of leaflet showing exudation of gum mass outside area with collapsed epidermis cells. Outer palisade cells resembling water storage cells (× 500). In the right corner is a photo of the small pore leading from the collapsed cells to the gum mass (× 2000). — b. Margin of leaflet with collapsed and non-collapsed cells. — c. Epidermis, on the right, with normal cell, all other cells collapsed and empty or filled with dark substances. On the left side of a degenerated stomatal pore (arrow) is a gum mass outside epidermis (b–c, semipolarized light, × 500).

Outline of stem anatomy

The epidermis is multiple with 2–4 cell layers. The green cortex appears storied consisting of 5–6 regular layers of palisade parenchyma which, however, in the corners are interrupted by strong fiber strands (Plate XIV a). The existence of an endodermis is difficult to establish. However, a single layer of crystal cells surrounds the fiber

strands except on their interior side and continues between the strands as a single layer of tangentially stretched living cells developed on the adaxial side of the storied palisade tissue. We believe that this cell layer represents the endodermis and, consequently, that the fiber strands belong to the primary phloem.

In older stems aggregates of small sclerified cells occur. These cells showed lignification of single wall layers and parts of the middle lamellae.

In one part of our material a cavity was found in the cortex. This was produced by the activity of a parasitic fungus which in a mature stage occurred as groups of globular cells. The walls lining the cavity were lignified and the surrounding living cells had hypertrophied nuclei.

The secondary xylem is uniform in the first growth ring. In the second, however, larger vessels occur diffusely arranged in aggregates. The rays are uniseriate. The pith parenchyma is made up of large thin-walled cells (Plate XIVa). Some of its cells, however, have thicker walls and a granulate contents. They are axially elongate and occur in groups or singly.

The epidermis deserves special, attention; further, the system of fiber strands and the increase in girth are of interest as well as the contents of crystals.

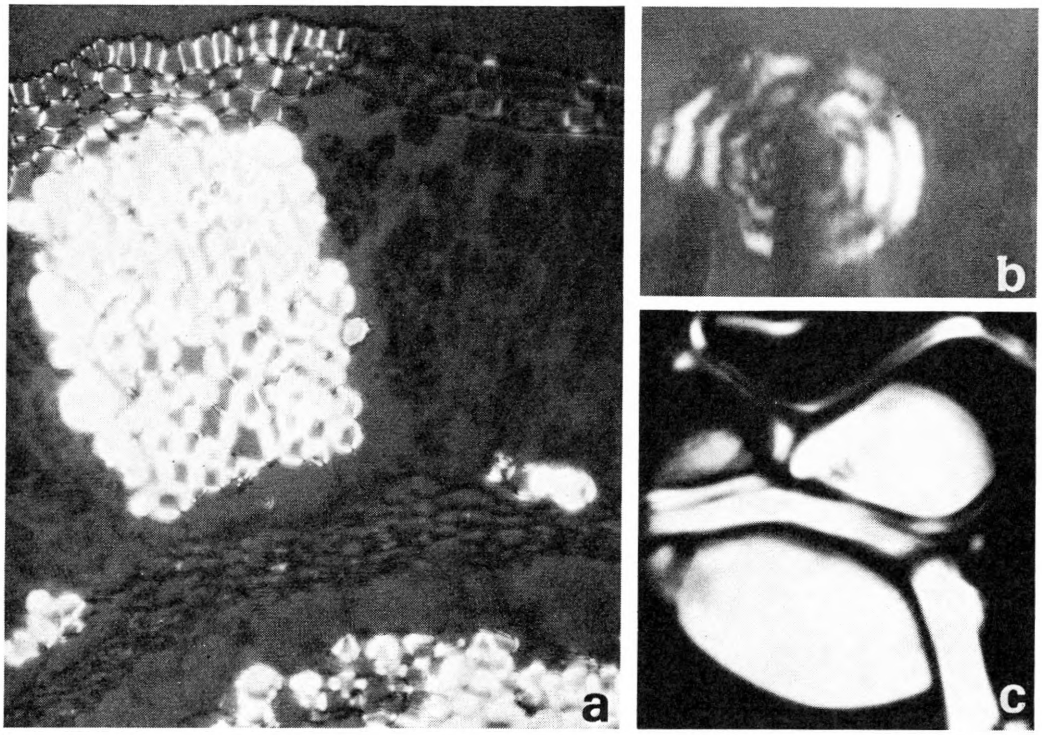


Fig. 38. *Prosopidastrum globosum*. a. Cross section of rib in polarized light. Fibers and xylem bright; small isolated fiber strands separated from larger mother-strand on both sides of its abaxial part. Cells in multiple epidermis relatively young and not showing up as much as those in the unilayered epidermis of the rib (× 320). — b. Young sphaerite with concentric layers. — c. Old very dense sphaerite in xylem vessels (b–c, polarized light, × 2000).

Fiber strands

In the younger stems a definite number of fiber strands occur in the corners inside the ribs. These strands undoubtedly accompany the primary phloem and are placed outside the protoxylem. There are 6–9 such primary strands. In older stems, however, a number of secondary strands are found in the interior part of the green cortex. In one case there were 9 small secondary strands between the primary ones. The secondary fiber strands are not surrounded by an endodermis and do not reach the epidermis. However, they are derived from the primary strands and issue from the adaxial side of the latter. First the primary strand gets one or two ear-like extensions in the adaxial part, next these extensions separate from the main fiber strand to form secondary strands (Fig. 38a). Sometimes an ear-like extension is prolonged and separates into two small fiber strands.

Epidermis

The multiple epidermis is clearly an active tissue which is able to follow the increase in girth which accompanies the secondary growth. New cells are inserted and in the peripheral layer old cells die, become empty and may get cutinized or suberized wall lamellae. The outer cells are covered by cutinized wall layers which, however, peel off in the areas between the ribs. The stomata are all placed in the areas between the ribs.

By comparing stems of different age it appears that a one year old branch already has three cell layers, sometimes just two, and in areas outside the rib fiber strands one layer only. The epidermal cells are radially stretched and their cuticle is provided with many sharp ridges. In a two year old stem the cells covering the ribs are frequently divided into two small rounded cells. Apart from the cells bordering the guard cells, the epidermal cells in the areas between the ribs are tangentially stretched resembling phellem cells and like these cells arranged in radial rows. Both anticlinal and periclinal divisions take place. There are four, sometimes five cell layers.

The peeling off of the cutinized outer walls is very conspicuous, but it rarely involves the areas next to the stomatal openings. When observed in SEM pictures these appear as roundish holes surrounded by a circular depression. The holes are pores in a thin diaphragm which is developed in continuation of the outer ledges. These ledges are formed outside the outermost epidermal cells in continuation of the outer walls of the guard cells (Fig. 39a). A striking feature is the variation in the diameter of the pores, which may be regulated by the cells surrounding the front cavity. It is not possible to decide whether the size of the aperture is determined during the final stage of the development of the stomatal apparatus, or whether the pore might be narrowed later as a response to changes in the degree of moisture. The latter process is not unlikely when the activity shown by the surrounding epidermal cells is considered (Plate XIVb–c).

The peeling off of the cutinized layers is anticipated by a lamellation. The outer layers are loosened and probably give rise to the roundish white bodies seen on SEM

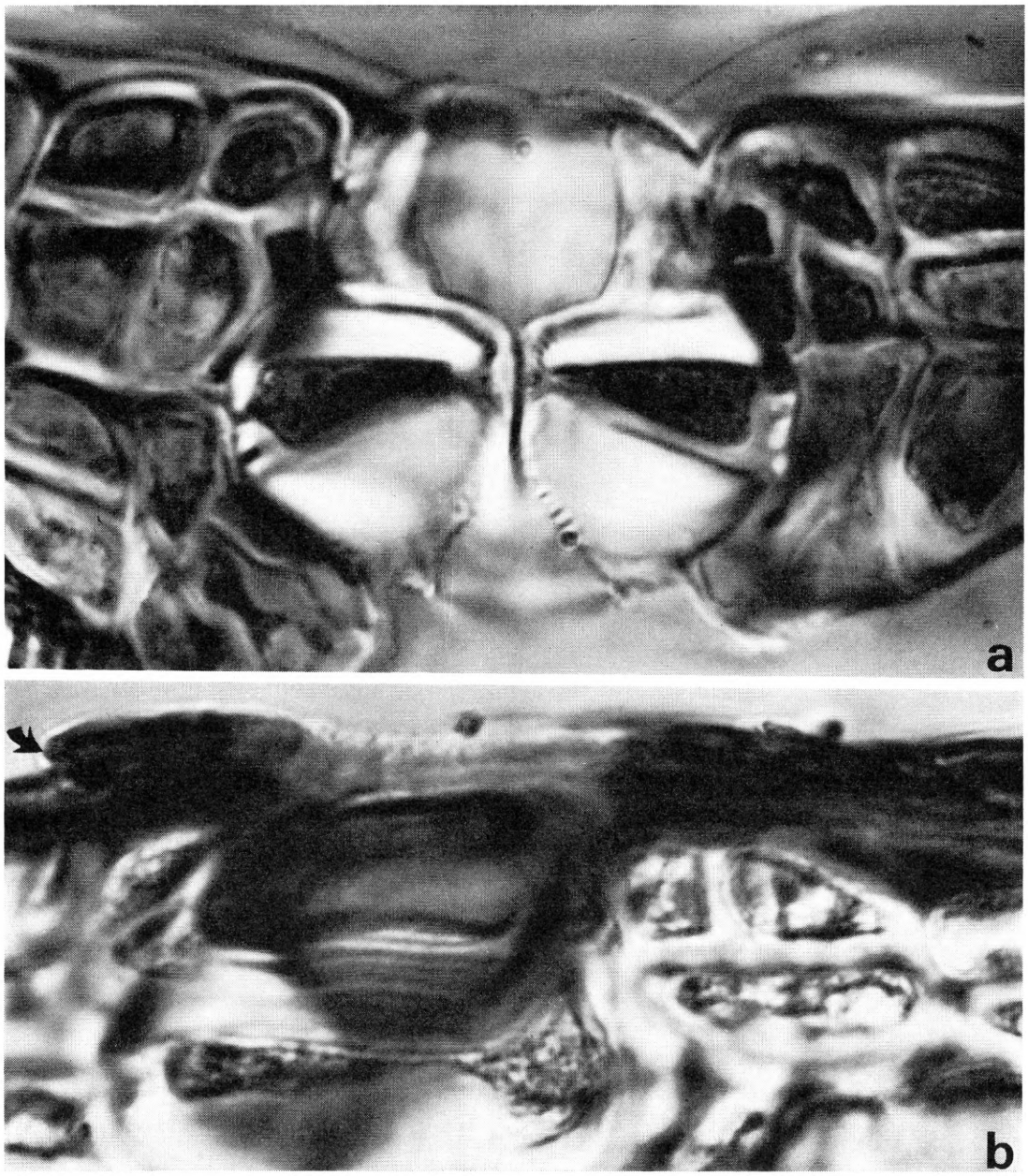


Fig. 39. *Prosopidastrum globosum.* Stomatal openings and multiple epidermis. Interference contrast. a. Cross section, Safranin-Fast green staining — b. Longitudinal view, Sudan IV staining. Striation of walls facing stomatal pore evident. In (b) (arrow) peeling off of cutinized outer wall (× 2000).

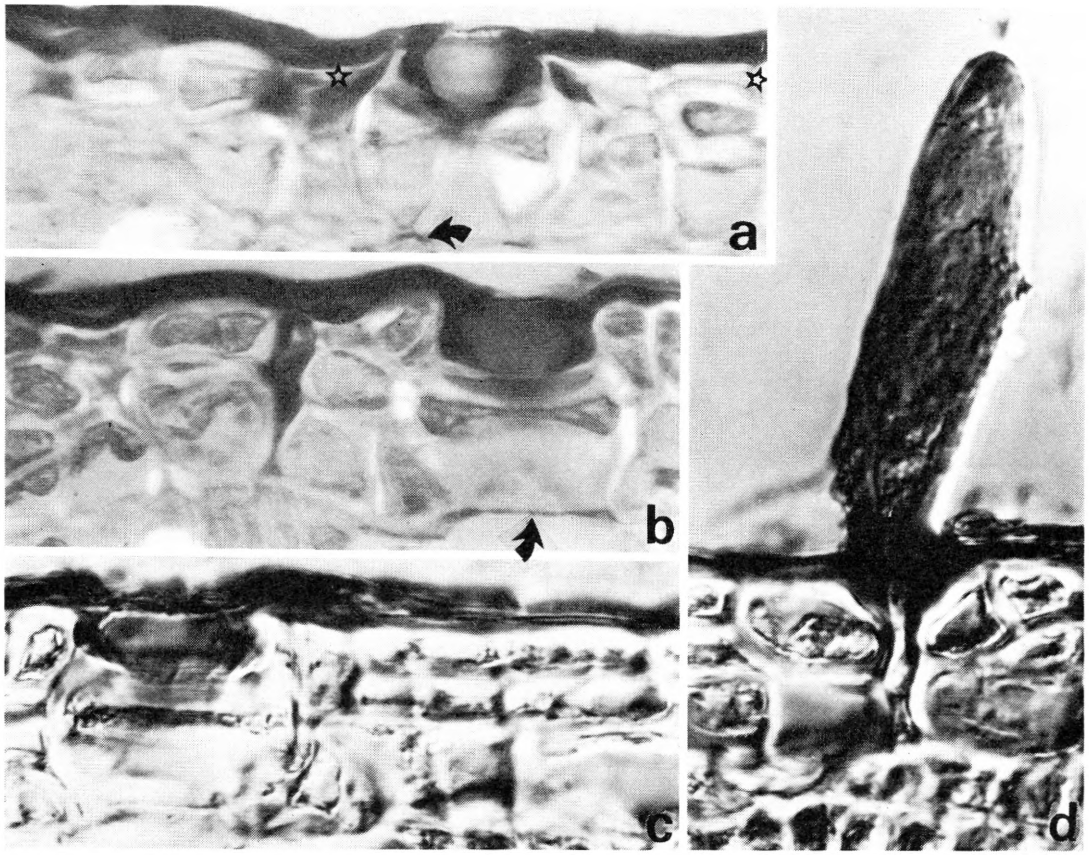


Fig. 40. *Prosopidastrum globosum*. Longisections of stem. Sudan IV staining. Behaviour of multiple epidermis and cuticular layer. — a–c. Peeling off of cuticular layer taking place and cutinization of walls of dying cells; outer parts of walls towards stomatal pore also stained, even small inner ledges (arrow). Small empty crushed cells at ★, — d. Unicellular cutinized hair with narrow cutinized rooting part reaching hypodermis. — a–b. Semipolarized light (× 320), c–d. Interference contrast (× 800).

pictures (Plate XIVc–d). At the same time as the outer epidermal cells produce cutinized layers, some of the cells die and this dying off is partly accomplished by a cutinization or suberization of a lamella in their walls and partly by a cutinization of the walls of the next cell layer, see Fig. 40. Trichomes are rare; they are unicellular and cutinized also in the narrow basal part which is inserted like a root between the epidermal cells (Fig. 40d).

The hairs often contain much cytoplasma in the basal swollen part. They may stay alive. The basal part is provided with a very thick cuticular covering which continues in the cuticular layer of the surrounding epidermal cells. The upper part has a thin somewhat warty cuticle covering about four wall layers of cellulose which are traversed by delicate radiating striae running from the cell lumen to the cuticle.

The structure of the stomatal apparatus appears from Fig. 39a–b, Fig. 40a–c, and

Plate XIVf. The walls of the front cavities are completely cutinized and the outer walls of the guard cells outside the central pore have a cuticular layer which is 1–2μ thick. The thick inner guard cell walls are covered by a very thin cuticle, but the small inner ledges are entirely cutinized at the substomatal chambers. Using interference contrast it becomes obvious that the guard cell walls facing the bottom of the front cavities and the areas between the central pore and the inner ledges are striated. This structure which resembles that found in *Fabiana* (p. 54) is probably due to lengthwise running, very low grooves (less than 1μ). The majority of the thick guard cell walls are built up of cellulose. The walls towards the front cavities measure 3–6μ while those towards the substomatal cavities are 5–10μ thick. The relatively thin walls towards the central pore and the subsidiary cells seem also to have a number of grooves. There are many subsidiary cells. Two rows of such cells, all narrow and curved, are surrounding the stomatal areas (Plate XIVf).

Calcium oxalate crystals

As already mentioned prismatic calcium oxalate crystals occur regularly in the majority of cells in the cell layer which like an endodermis surrounds the original fiber strands inside the ribs in the corners of the stem. In younger stems from the Atuel material (No. 1393) this type and position of crystals were dominating, but in several cells a formation of sphaerites was taking place (Fig. 38b–c). Sphaerites were initiated in green cortex cells, sometimes in epidermis and fiber cells, phloem parenchyma cells, and in vessels. In the initial phase small groups of needle-shaped crystals are arranged radially with intervals in concentric layers, which again are spaced from one another by circular zones without crystals. Next the radial crystal groups merge and form circular zigzag bands. The final stage was studied in two year old stems from the same area. Here the sphaerites were very dense, the concentric layers were not spaced but were still possible to detect, also sometimes a radiate structure. By using polarized light a dark cross appeared as in starch grains. In many cases the sphaerites filled the whole cell. They always started their growth from the cell wall. According to KÜSTER (1956) such sphaerites consist of monohydrate ($Ca(C_2O_4)$, 1 H_2O). They were not formed in the cells containing prismatic crystals, but very often sphaerite-cells were placed singly or in aggregates near the cells with prismatic crystals. In the Uspallata-material no sphaerite formation was observed.

Prosopis sericantha Gill. ex. Hook. & Arn. (Mimosaceae)

Material: W. Argentina, Santiago del Estero, near Termes de Rio Hondo. Böcher, Hjerting & Rahn No. 2460, Jan. 20, 1956.

Occurrence and morphology

The species occurs in subtropical and dry parts of Argentina, viz. in the provinces: Tucumán, Santiago del Estero, Catamarca, Córdoba, San Luis, and the northern part of Santa Fe, cp. BURKART (1940 pp. 84–85 and Plate 8).

The material was collected on an excursion from Tucumán. *Prosopis sericantha* grew in typical dry subtropical forest (Chaco) interrupted by dry *Larrea* shrub steppe (Monte). It is a 1 m. tall shrub without leaves, but with opposite scale leaves supporting branches which terminate in thorns. The surface of the green branches is glabrous, although at the base of young branches there may be a few projecting hairs. Also the margins of the scale leaves have a few hairs. In the material at hand the scale leaves support branches which usually get suppressed or reduced, while two opposite branches of third order issuing from the base of the suppressed branch develop. This curious type of branching was studied further in cross sections of the stem.

Outline of stem anatomy

Plate XVd shows the main features. Inside the epidermis follows a layer which in all respects resembles a hypodermis. The hypodermis is interrupted by the deeply sunken guard cells. There are 5–6 rows of green palisade cells under which follows a layer, probably representing the endodermis, in which almost all cells contain a crystal. In the palisade tissue groups of cells contain solitary twin crystals. Some of the phloem parenchyma cells and the cells in the axial parenchyma also contain crystals.

The green tissues are interrupted by numerous fiber strands. In cross sections 18–20 large and about 9 small strands can be counted. On their abaxial side and towards the green cells they are limited by a layer with many crystals, presumably the endodermis which bulges outwards and which outside the larger strands reaches the hypodermis. The fiber strands are placed in a peripheral circular area. They support low ridges which are easy to see in SEM pictures at low magnification (Plate XVa).

The wood is storied and with concentric wide bands of fibers. There are many rays, mostly uniseriate (see p. 80). The cell walls of the pith parenchyma become rather thick and lignify.

Epidermis

There is a striking discrepancy between pictures obtained with the light microscope and SEM micrographs of the surface of the stems. This difference is due to the presence of a complex wax pattern on the surface which disappears in material treated with alcohol for microtoming and staining. Plate XVa–c shows the wax deposits, and Plate XVIa–b and Fig. 41a–b the smooth surface as observed in the light microscope.

The stomata have their long axes transversely to the main axis of the stem and they are arranged in longitudinal depressions between the low ridges mentioned above. The stomata are deeply sunken and near the ridges they form longitudinal groups resembling staircases and transversal groups usually of two stomata in depressions (Plate XVa–b). This stomatal pattern contributes considerably to the irregular impression of the surface. Another complication appears from SEM micrographs of the stomatal front cavities (Plate XVc). These cavities may resemble underground

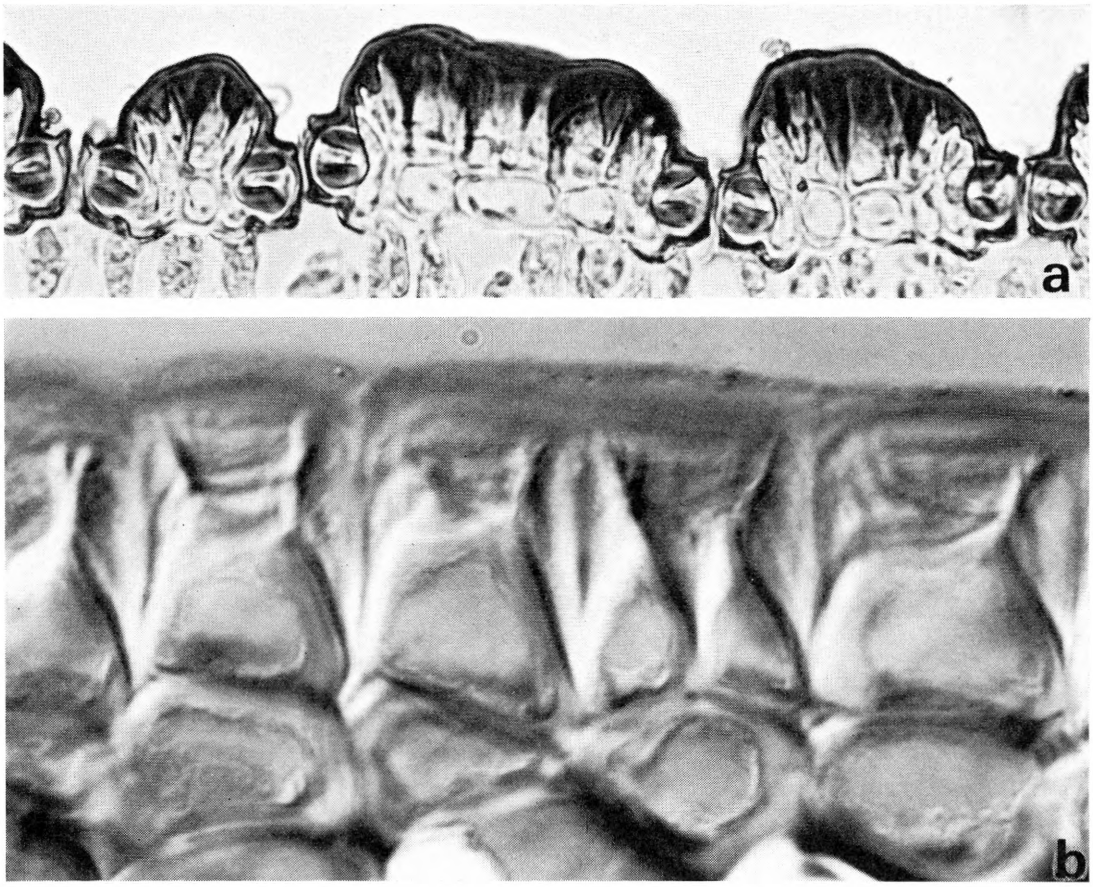


Fig. 41. *Prosopis sericantha*. a. Longisection of stem cutting through four closely spaced stomatal openings separated by outbulging cutinized area, cp. Plate XV a–b. Sudan IV staining (× 800). — b. Part of epidermis. Interference contrast emphasizing lamellation of outer wall and narrow extensions with brushes of delicate channels (× 2000).

caverns with stalactites. The wax clearly forms protuberances and sharp crests, and these wax figures seem to be formed outside a system of microscopical channels which are seen in microtome sections and become particularly clear when using interference contrast (Fig. 41 b, Plate XVI a). Possibly such micro-channels continue in cuticular pores as those described by HALL (1967: fig. 13).

In mature stems a good many epidermal cells are narrow and elongate. The original epidermal cells divide into two (four) cells which have their long axes stretched radially like the palisade cells beneath. Occasionally also periclinal walls are formed and thus very locally a multiple epidermis. The sister cells in the outer layer form small colonies and the outer layers of the thick cuticular layer often bulge over each colony. While broader epidermal cells may taper into two or more groups of micro-channels, the narrow ones including the subsidiary cells usually taper into a single one,

which in its distal parts divides into a brush of very fine channels (Fig. 41 b, Plate XVI b). The cuticular layer has very deep cuticular flanges almost reaching the hypodermis (Fig. 41 a). The outer walls in this layer and sometimes even parts of the interior walls are often ± cutinized.

The outer walls of the epidermal cells are clearly lamellated. In the inner parts which are traversed by the delicate channels the lamellae are most conspicuous (Plate XVI a), but they can also be traced in the outer parts of the walls where the channels may be submicroscopical. In alcohol—preserved material the wax deposits on the surface have almost completely disappeared. Remains of wax were observed in some of the front cavities and in shallow depressions outside transverse walls.

The crescent subsidiary cells are accompanied by 1–2 narrow cells which in their outer part contribute to the formation of the front cavity. The guard cells are small as compared to those in most other species mentioned in the present paper. Even *Prosopidastrum globosum* (Fig. 39) has much larger guard cells. The thick walls of the guard cells stain with Sudan IV. They have a cuticular layer towards the pore, the front cavity, and the substomatal chamber, but furthermore their secondary walls react to the dye (Fig. 41 a) and must be cutinized. However, the secondary walls are also stained with Safranin (Plate XVI b), a fact which suggests incrustation with lignin. According to our experiences lignification of guard cell walls is very rare in angiosperms, while it is common among the gymnosperms.

Periderm

Phellogens are formed in the epidermis, the hypodermis, and in the green cortex cells. The periderm formation frequently takes place near the fiber strands and succeeds ruptures in the epidermis resulting from the dilatation growth of the cortex. If the epidermis ruptures outside a fiber strand, a phellogen will incurvate and cut off the entire strand and the layers outside. In certain cases some of the epidermal and hypodermal cells outside a strand are transformed into phellogen cells, and the phellogen formation continues in the cortex cells next to the adaxial part of the fiber strand. The phellem which is formed fills out and widens the ruptures and gaps in the epidermis, but in such cases the fiber strand is maintained although it will be surrounded by and finally embedded in the periderm.

Additional periderms are sometimes formed in the cortex beneath the ones formed previously and even deeper. Locally a rhytidome may be formed which fills out deep cracks involving the secondary xylem. In such cases phellogens seem to be formed by transformation of axial parenchyma bands.

Fibers

The cells in the phloem fiber strands are shown in Plate XVI c–d. As compared with those described in *Stillingia* (p. 8), they are much narrower, 7–8μ in diameter as against 17–18μ in *Stillingia*, and they are not so distinctly lamellated. On the other hand,

older fiber cells appear regularly and transversely striated and this character seems not to be a result of dislocations during their growth (cp. Plate XVIc). As compared with the xylem fibers, the phloem fiber cells are longer, wider, and with more and more distinct wall layers. The xylem fibers do not show any signs of transverse striation and their inner younger wall layers shrink as a result of fixation.

Rays and branch primordia

The xylem has numerous rays which are mostly uniseriate, more rarely biseriate. However, where two opposite lateral branches issue from the stem, the rays placed inside such branches become much wider. Sometimes one of the branches in a pair is completely suppressed. Where such a branch might have developed, the ray inside has about four rows and includes a small vascular strand which resembles a cortical bundle. Scars from branches which are shed or die early have thick coverings of periderm. Outside the broadest rays three buds may develop, a median corresponding to a branch of first order, and two lateral ones which are of the second order. All buds are protected by scale leaves. These are thick along the middle vein and very thin on both sides. Many cells in the marginal parts contain crystals. In the axils of the scale leaves resinous substances are formed. They are probably excreted by clavariform glands arranged in pairs. In other cases the median bud fails to be formed. Instead two late-coming buds of second order appear outside a wide ray; their main axes diverge from the axis of the suppressed branch by 35°–40°.

Junellia glauca (Gill. & Hook.) Moldenke (Verbenaceae).

Material: W. Argentina, Prov. Mendoza, Salado Valley, Co. Choiques, 1750 m. above sea level. Böcher, Hjerting & Rahn No. 1238, Nov. 27, 1955 – Atuel Valley, Campamento Atuel, 2300 m. Böcher, Hjerting & Rahn No. 717, Oct. 31, 1955.

The material from Co. Choiques was determined by Dr. N. Troncoso. The Atuel material is deviating and collected early in the season. A careful comparison makes it evident that the plants are closely related to typical *J. glauca*. They may belong to a separate taxon, but the available material is insufficient for a thorough taxonomical treatment. In this connection the anatomical differences mentioned below are of interest. In any case *J. glauca* is a polymorphic species.

Occurrence and morphology

Junellia glauca grows abundantly in several places in the southern part of the Mendoza province as well as in northern Neuquén. It prefers gravelly calcareous soil and is frequently dominant e.g. together with *Cassia kurtzii* or *Colliguaya integerrima*; details in Böcher, Hjerting & Rahn (1972, pp. 228—229, 256—258).

J. glauca is a low shrub, often a dwarf shrub with assimilatory, mostly upright branches and few narrow leaves with more or less revolute margin and retuse apex. The flowers are clustered in head-like terminal inflorescences.

Leaf anatomy

The leaves on the material of typical plants from the Salado Valley (No. 1238) are dorsiventral and have revolute margins. They carry scattered trichomes, setae and stipitate glandular hairs. The latter are particularly common in the bottom of a furrow situated above the middle vein (Fig. 44 a). Between the bundle and the furrow chloroplasts are absent in the cells which are rather large and with irregularly corrugated walls. A much wider area of such cells also occurs between the phloem of the bundle and the hypodermis of the underside. The stomata are placed on both sides but are very rare in the areas on both sides of the middle vein.

In the deviating material from the Atuel Valley (No. 717) the leaves were very young and not yet revolute. Nor was there any furrow over the middle vein. Instead the whole leaf was often groove-shaped. On the upper side the areas inside the leaf margins were clearly growing, and in some of the leaves the outermost parts near the edges were bent downwards. The palisade cells were differentiated but still short. The hair cover was much denser but consisted also of setae and glandular hairs some of which, however, were sessile. On both sides of the middle vein the same large non-assimilatory cells occurred as in No. 1238, but here the walls were normal and the cells appeared to have been turgescent. As these cells occupy a semicircular area below the middle vein, they may in a turgescent stage contribute to keep the leaf blade distended. On the other hand, if the cells are not turgescent and have corrugated walls, the leaf may return to a position of rest. In older leaves with revolute margins a movement of this kind may result in a variation in the degree of incurvation of the margins and thus the size of the exposed part of the underside. This area will probably be wider in moist periods when the large cells are turgescent.

Outline of stem anatomy

The epidermis has one layer of cells. Just below there are hypodermal cells alternating with groups of strong fiber cells, usually in one layer, but sometimes and particularly outside the phloem fiber strands the peripheral cortex fiber cells are arranged in two layers. The stomata are found outside the intervals in the cortex fibers (Fig. 42), and their long axes are oriented transversely to the main axis of the stem. Inside the cortex fibers a many-layered palisade chlorenchyma forms a continuous layer which towards the stele is limited by a continuous endodermis. The perivascular phloem fibers occur in a number of strands situated inside the very blunt and indistinct ribs which can be seen in surface views of the stem (Plate XVII a). Also the phloem and the xylem form continuous cylinders. The protoxylem groups project a little into the pith. Between these protoxylem ridges perimedullary fibers occur. On the

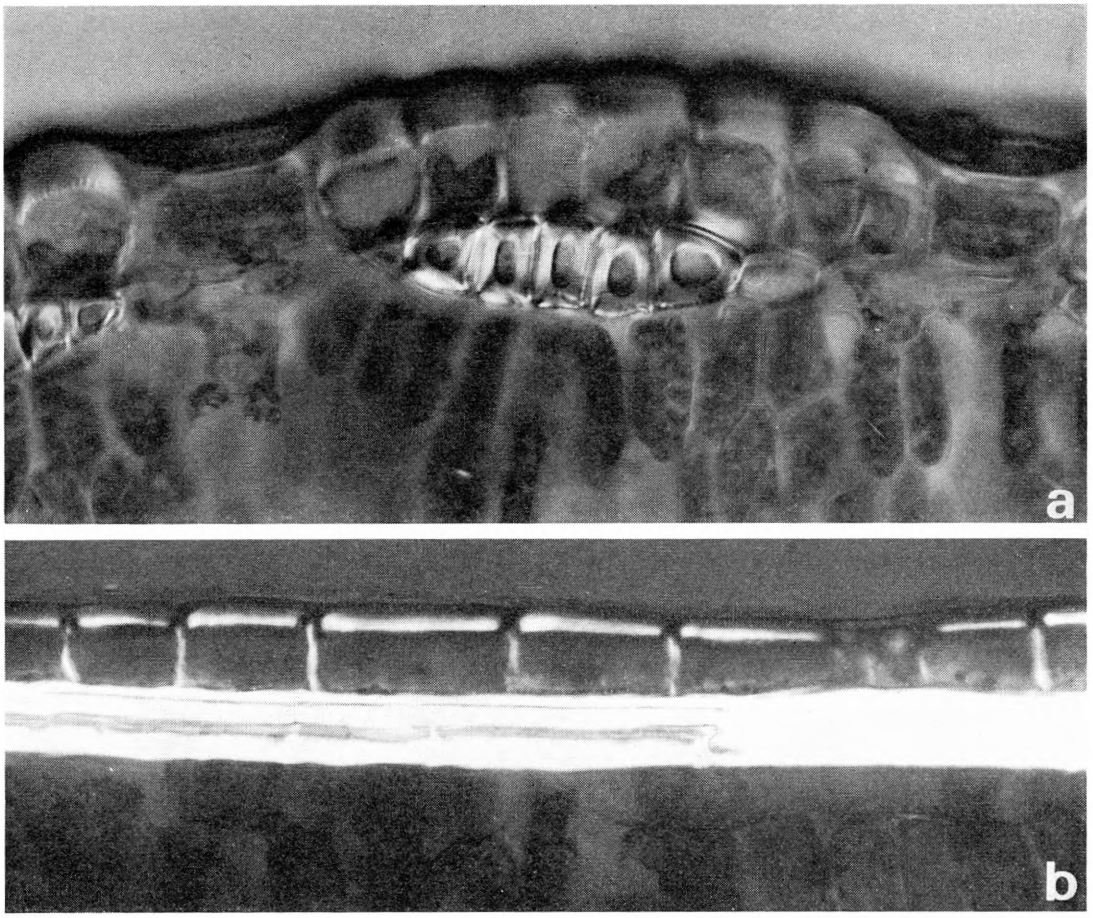


Fig. 42. *Junellia glauca*. a. Cross section of stem showing position of fiber strands which support the low ridges between very shallow stomatal furrows. Radiating structures in the adaxial part of outer wall in the far left epidermis cell. — b. Longisection through low ridge. The fiber strand shows up in polarized light as do the adaxial part of the outer wall and the anticlinal walls of the epidermal cells (× 500).

adaxial side of the protoxylem and these fibers the pith cells are axially elongated and with fairly thick walls. The central pith cells are short and wide.

Epidermis

The epidermal cells have thick outer walls but deviate from those in most other species we have studied by the comparatively low degree of cutinization. The cuticle and the outermost wall layers stain with Sudan IV, and the inner wall which consists of cellulose shows up brightly in polarized light (Fig. 42). In the innermost part of the wall radiating micro-channels are sometimes distinct.

The outer wall undergoes considerable chemical changes in parts where the

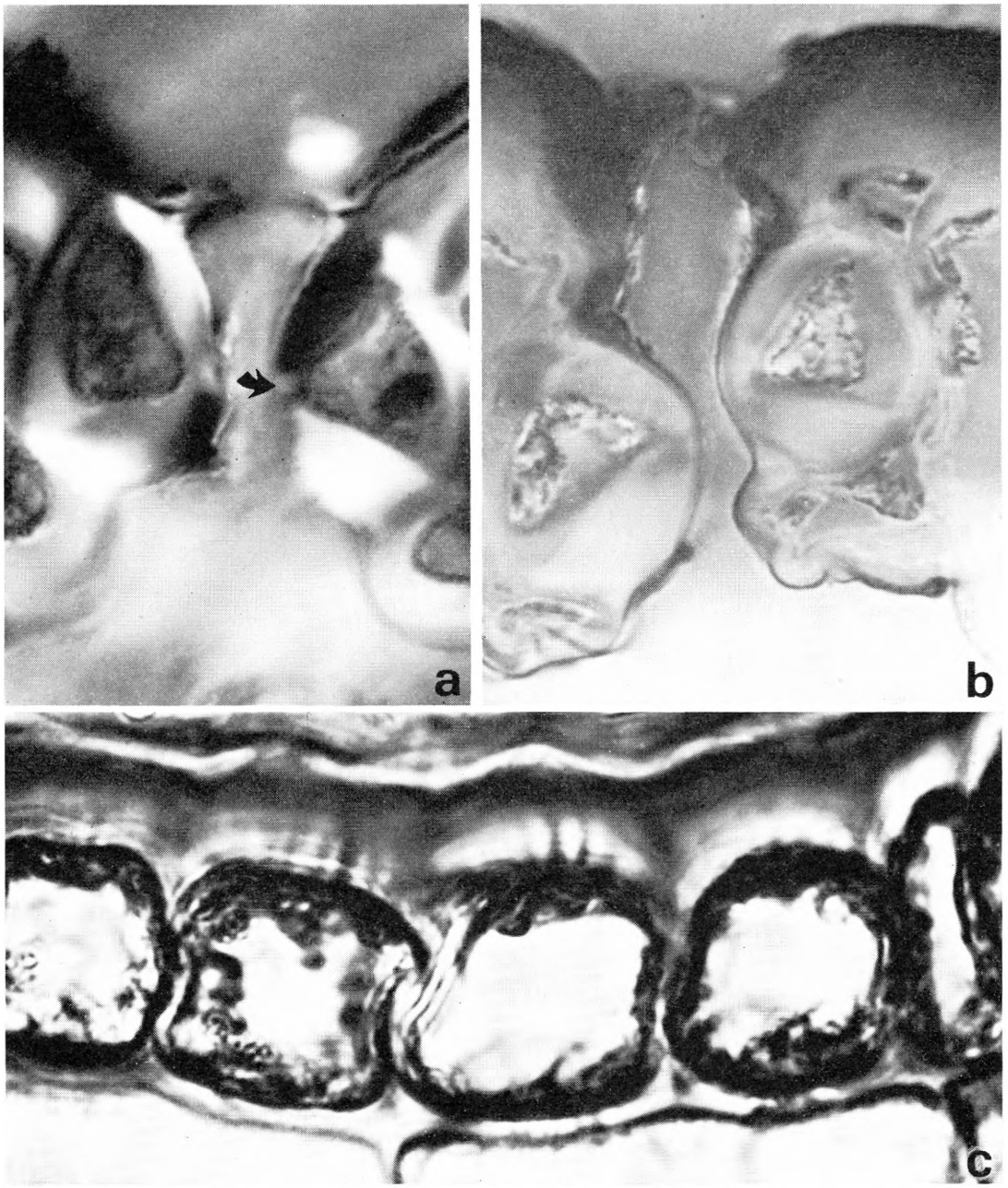


Fig. 43. *Junellia glauca*. a. Stomatal pore. A furrow outside narrow part of guard cell (Safranin-Fast green, interference contrast, × 2000). — b. Stomatal pore in semipolarized light, Sudan IV stains walls of front cavity as well as inner ledges of which the right hand one is displaced. Birefringence in front cavity is probably due to wax (× 2000). — c. Chemical alterations in outer epidermis walls. Cuticula bright. Below is a wall area which stains red with Safranin as do the lamellae and the radiating wall areas near the cell lumina (Safranin-Fast green, polarized light, × 2000).

subepidermal cells become suberized or a periderm is formed below. The epidermal cells in question waste away, but before they die, the thick cellulose part of the outer wall gets distinctly lamellated in its interior part, while the outer part bordering the cuticular area seems to lignify. With Sudan IV the whole wall inside the cutinized area remains unstained, but with Johansen's quadruple stain the Safranin component stains the outer sector of the formerly cellulose part which, therefore, probably is lignified. Also some narrow wedges through the inner wall areas are stained and may represent fissures or larger channels incrusted with lignin (Fig. 43c). The lamellation in the innermost parts of the walls is interesting. In normal cells Fast-green stains these parts homogeneously green. But in the deviating cells the walls are alternately green and white. The walls appear to be a little thicker than usual. We assume that the white lamellae are newly formed and inserted between older green cellulose lamellae. As they remain unstained also with Sudan IV, they may consist of e.g. pectic substances. The radiating reddish stained areas are formed primarily in those parts where very numerous radiating micro-channels can be seen in normal walls. A development from such delicate structures to the coarser radiating ones could not be followed but is not unlikely.

The surface varies greatly. In material No. 1238 the surface appears finely striated and granulated, while in No. 717 it is smooth with some cracks, and the striae which occur outside the peripheral fibers are very indistinct (cp. Plate XVII).

The surface view of the stomatal openings also unveils an interesting difference between the two strains. In No. 1238 (Plate XVII a, b, c) the openings are situated in small depressions, while in No. 717 no sinking down was found (Plate XVII d, e, f). In both strains the subsidiary cells bulge out beneath the guard cells, and the outwards bulging parts have rather thick cuticular coatings (Plate XVII c, f). In both the substomatal chambers are asymmetrical. This is particularly the case in No. 1238 (Fig. 43b and Plate XVII c). A similar asymmetry is found in *Diostea juncea* (cp. Figs. 46 and 48b).

The front cavities are very different. In No. 1238 the outer ledges are small, but the cuticular parts of the walls facing the pore are able to increase in thickness so that finally the pore is reduced to a narrow fissure (Plate XVII c). In No. 717 the outer ledges are larger and there is a typical front cavity, but in almost the same way as described in *Prosopidastrum* the outer ledges are able to grow towards one another to form a diaphragm through which a minute opening leads into the front cavity (Plate XVII d, e, f).

Observations in polarized light using the Red I plate indicate that in material No. 1238 wax may be excreted on the surface as well as on the sides of the pore (Fig. 43b).

The guard cells in No. 717 are larger than those in No. 1238. The distance between the outer and inner ledges is about 22–25μ in 717 and 15–19μ in 1238. A similar difference in size is found in many plants with cytotypes on different ploidy-levels.

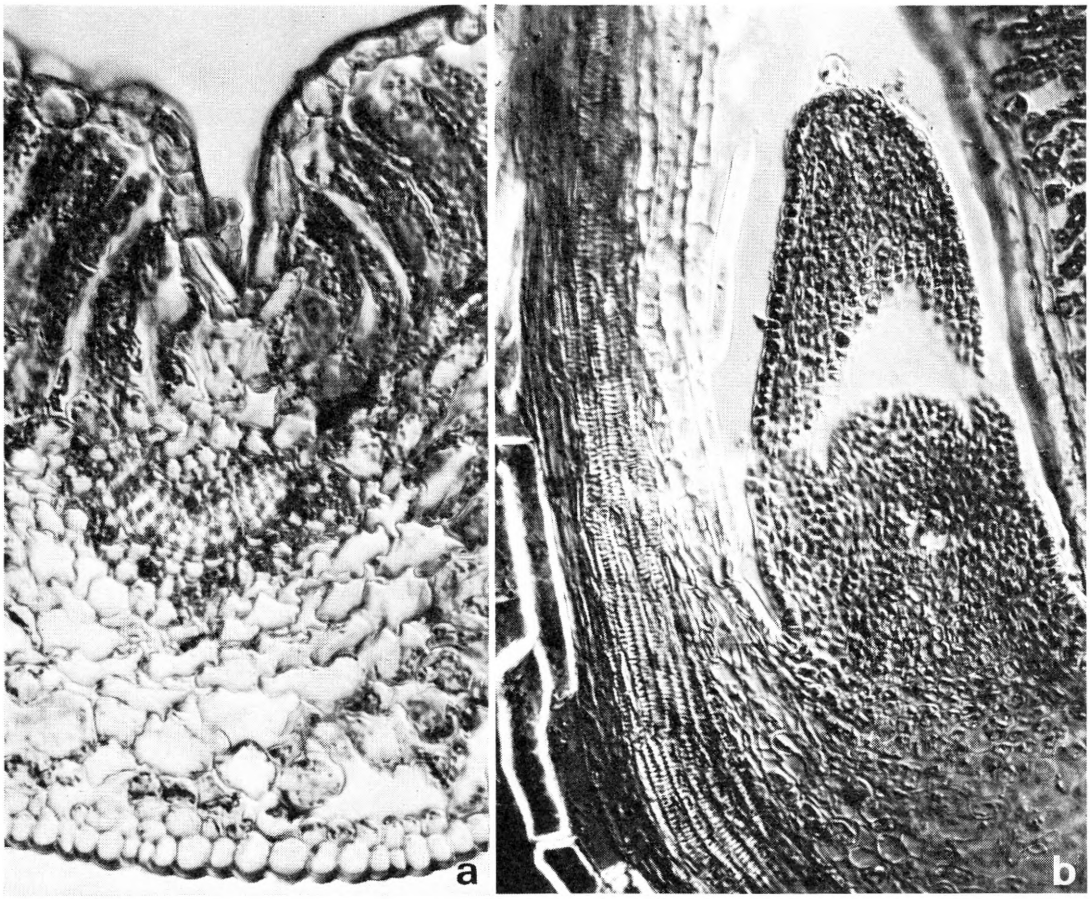


Fig. 44. *Junellia glauca*. a. Cross section of leaf at middle nerve. Furrow with gland in bottom and shrunken large cells on both sides of vein. — b. Axial bud covered by leaf; on the right palisade tissue in stem, on the left supporting leaf with central vein, elongate bundlesheath cells on abaxial side outside phloem (a–b. Safranin-Fast green, interference contrast, ×240).

Nodes, axils and branch primordia

The bases of the opposite leaves are persisting and become protected by periderm. The whole node may be covered by suberized cells. Sometimes the basal parts of degenerated axial shoots are maintained, and basal parts of such shoots with their basal scale leaves are also covered with periderm. Phellogens arise in the subepidermal layer or a little deeper, but the cork formation is normally restricted to the nodes.

The persisting leaf bases are traversed by a vascular bundle which sometimes goes through an abscission cork layer and continues a little outside this layer, where it is surrounded by decomposed leaf cells only. On its abaxial side the leaf trace is followed by a fiber strand which is a continuation of one of the perivascular fiber strands.

In the proximal part of the leaf base the fusiform fiber cells are replaced by elongate parenchymatous cells with rather thick walls forming a sheath (Fig. 44b).

Branch primordia are regularly found in the axils behind the persisting leaf bases. The apical meristems are protected by a leaf which forms a cup (Fig. 44b). On the adaxial side of the leaf base as well as on the top of the protecting primordial leaf many unicellular trichomes are present. All of them taper upwards, contain cytoplasm and nuclei, and have non-cutinized walls; even the walls of the hair bases consist of cellulose. At the bottom of the narrow furrows, between the leaf base, the primordium, and the main axis the epidermis is made up of very small cells which may be almost meristematic. Occasionally stipitate glands are situated at the bottom.

It has to be investigated experimentally whether the axils, which here are formed like pitchers, can collect water, and whether water uptake is possible through the non-cutinized hairs and the epidermis in the bottoms of the axils.

It is clear from our observations, that uptake is only possible in such axils where primordia are present and the leaf base cells, apart from the abaxial suberized ones, are still living. In a later stage all cells surrounding an axil are dead and suberized. The leaf bases may even be shed after the formation of a new abscission cork layer which occurs just where the leaf base issues from the main axis.

Verbena scoparia Gill. & Hook. (Verbenaceae)

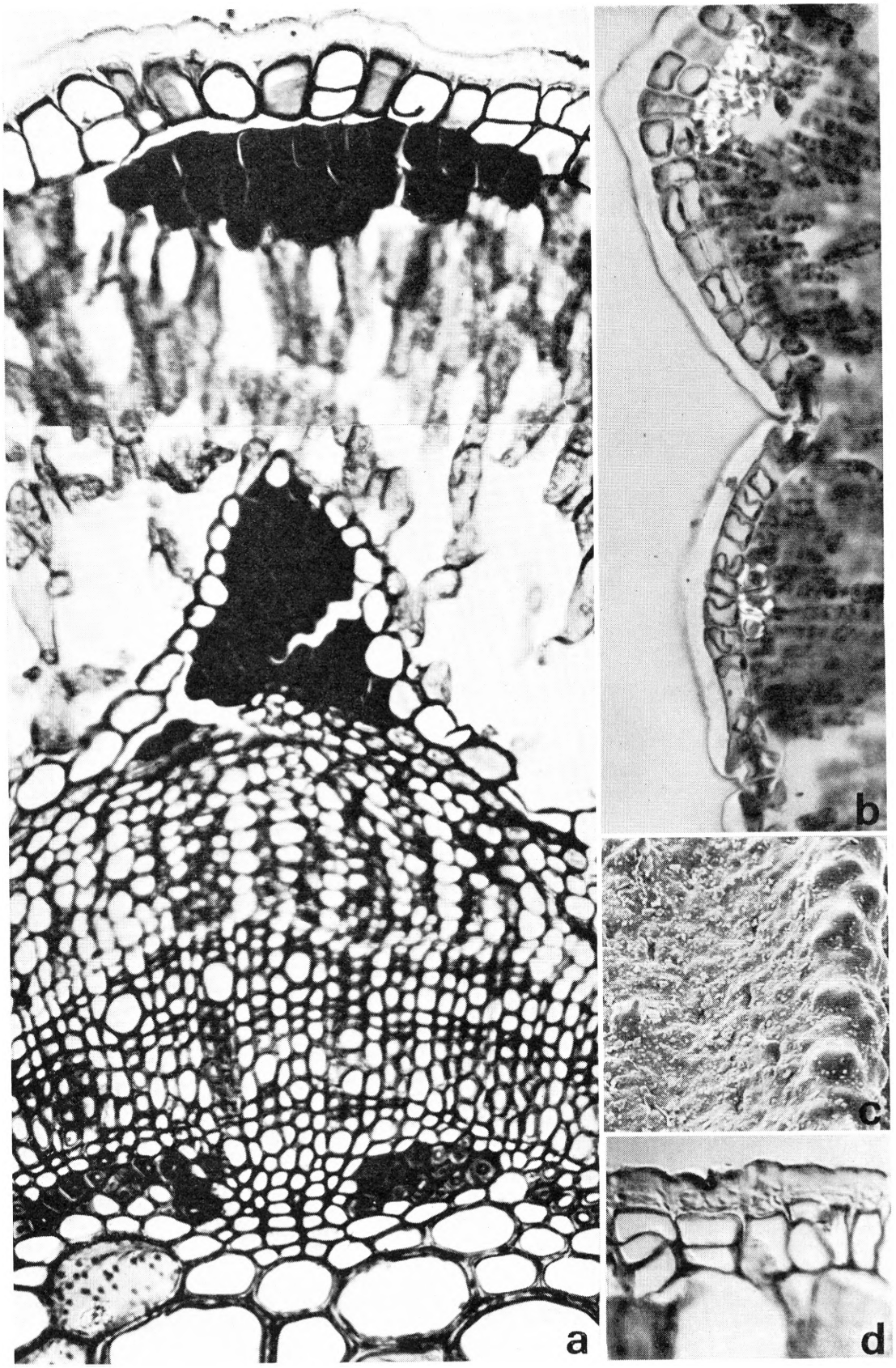
Material: W. Argentina, Prov. Mendoza. Near San Rafael, 1200 m. above sea level. Böcher, Hjerting & Rahn No. 1143, Nov. 22, 1955.—Above Villavicencia, 2150 m. above sea level. Böcher, Hjerting & Rahn No. 2120, Jan. 1, 1956. Dr. N. Troncoso referred No. 1143 to var. *puberula* Troncoso, see Böcher, Hjerting & Rahn 1963 p. 109.—The species may also be referred to the genus *Diostea*.

Occurrence and morphology

Verbena scoparia occurs in rocks; in the case of No. 1143 from the San Rafael area it dominated the rock vegetation together with *Hyalis argentea*. At Villavicencia it also grew on rocks together with e.g. *Dipyrena glaberrima* and *Gymnophyton robustum* (cp. Mathias & Constance 1962, Böcher 1972). According to Roig & Roig (1969:22 and 27) *Verbena scoparia* dominates together with *Colliguaya integerrima* on not too dry rocky slopes (here facing south), but it is also an important plant on dry north-facing slopes along with *Mulinum spinosum* and *Artemisia mendozana*.

In vegetative characters *V. scoparia* resembles *Junellia glauca*. The branching is opposite, and the main shoot and the two branches may be almost equally strong and parallel. The surface is papillate and old shoots are more or less lilac-brownish. In *Junellia glauca* the surface is almost glabrous and the ribs less distinct. The orientation of the stomatal openings is parallel to the main axis of the stem in *V. scoparia*, while in *Junellia glauca* it is at right angles to the main axis (Fig. 45, Plate XVIIa).

Fig. 45. *Verbena scoparia*. a. Cross section of stem. Quadruple staining which stains cortical fibers, phloem fibers and perimedullary fibers intensely (× 500). — b. Cross section of stem in No. 1143 showing two deeply sunken stomatal openings (Safranin-Light green, × 320). — c. Surface view of rib and interrib area with stomata (SEM micrograph, × 195). — d. Multiple epidermis and wall lamellation (interference contrast, × 500).


a
b
c
d

Leaf anatomy

The small leaves are clearly isolateral with palisade cells on both sides; sometimes, however, some inclination towards dorsiventrality may occur. The epidermal cells are covered by a cuticle but the walls have no cuticular layer, nor any cuticular flanges. At the leaf margins some rather large cutinized cells occur and may be regarded as papillate hairs. The stomata are not sunken. The upper surface often carries some glandular hairs. They are short stipitate and the stipe cells are covered by thick cutinized walls. The heads contain up to 8 elongate cells which are covered with a common cuticle. At the top the cuticle is provided with a small circular hole.

Outline of stem anatomy

Troncoso (1957 fig. 2 and p. 170) described the stems of *V. scoparia*. They are octogonal, the blunt ribs being supported by cortical fiber strands. The stomata occur in the areas between the ribs. The green palisade cortex cells surround continuously the endodermis, but inside the ribs endodermis curves outwards surrounding another fiber strand which is perivascular (Fig. 45a). The green cortex is here three cells broad, while it may contain six layers on both sides of the perivascular strands. Midway between the corner perivascular fiber strands some smaller additional fiber strands occur. A layer of sclereids just inside the endodermis connects all the perivascular fiber strands. In the periphery, however, fibers are usually also formed outside the additional ones beneath the endodermis. A continuous phloem and xylem surround the pith which between the protoxylem groups develops a medullary sheath of fiber cells (Fig. 45a).

The endodermis seems to be ruptured at points outside the perivascular fiber strands. Sometimes, however, the green cells connecting the peripheral and perivascular fibers are placed in continuation of the endodermis on both sides. They may, therefore, be looked upon as radially stretched endodermis cells which here perhaps are transformed into chlorenchyma cells.

Exchange of substances between the vascular tissues and the green cortex seems to be easy enough in young stems where the fibers are not connected with sclerenchymatous cells. The endodermis appears neither to have passage cells nor Casparian strips, but large simple pits which connect the cells tangentially. Water and carbohydrates may therefore pass the endodermis without much control. On the other hand, in older stems just inside endodermis there is an almost continuous sheath of mechanical lignified cells which in spite of maintaining their nuclei may make such an exchange difficult and reduce it markedly.

Epidermis

In all our material the epidermis is one- or two-layered. Usually some of its cells divide so that it locally becomes multiple (2–3 layered, see Fig. 45d). In several characters, however, the material from the two collections differs from one another.

The surface is irregular and more or less cracked. Some of the epidermis cells

which cover the ribs have a particularly thick outer cutinized wall which appears as a series of warts on the ribs (Fig. 45c).

The warty appearance is less pronounced in material No. 1143. Another much more pronounced difference concerns the degree of sinking of the stomata. In No. 1143 the stomata are deeply sunken as a result of overarching subsidiary cells which have very thick outer cutinized walls (Fig. 45b). Surface views in SEM show the stomatal openings as fissures which are stretched parallel to the direction of the main axis (Fig. 45c). In No. 2120 the stomata are not so deeply sunken.

Cuticular flanges occur in the radial walls but they are much wider in the original or first formed walls. Obviously the flanges widen in connection with the increase in girth. During this growth wedge-shaped openings in the flanges develop and a number of lamellae become visible (Plate XVIIIb, c). New wall layers may be produced continuously until finally the openings in the flanges reach the surface forming an irregular crack. The cutinized part of the wall is always very thick, while the inner cellulose part is thin. In the most recent parts of the cutinized wall numerous radiating striae are seen (Plate XVIIIb, c) but also a distinct lamellation. Some of the lamellae show up in polarized light due to contents of cellulose. The lamellae are particularly clear in slides prepared with Johansen's quadruple staining. But the Safranin component in this mixture stains some of the lamellae red indicating lignification. As an explanation we might in this case assume a lignification of one or a few lamellae of cellulose or pectic substances near the border of the cuticular layer towards the interior wall layers.

In some cases fissures wedge right through the cuticular layer and reach the interior part of the wall where new wall layers are developed. The plant seems to respond to this by rapidly building up a completely new outer wall inside the fissure. During this process the new wall curves and gets thick in the middle. It becomes traversed by numerous radiating micro-channels and some of its layers lignify.

The outermost parts of the cuticular wall layer peel off; however, before doing so, they are maintained for some time as a porous irregular mass (cp. Plate XVIIIb).

Diostea juncea (Gill. & Hook.) Miers. (Verbenaceae).

Material: W. Argentina, Neuquén, Lake Nahuel Huapi, Lat. 41° S., Alt. 800 m. Böcher, Hjerting & Rahn No. 1719, Dec. 15, 1955.

Occurrence and morphology

Diostea juncea occurs at the eastern end of the great lake Nahuel Huapi together with *Discaria articulata* and *Adesmia coronioides* in dry thickets surrounded by Patagonian steppe vegetation (*Mulinum*–soc. rich in *Festuca pallescens*). Among the accompanying species may be mentioned *Fabiana imbricata* and *Mutisia retusa*.

Diostea juncea is a small tree or a tall shrub and not a true apophyllous species.

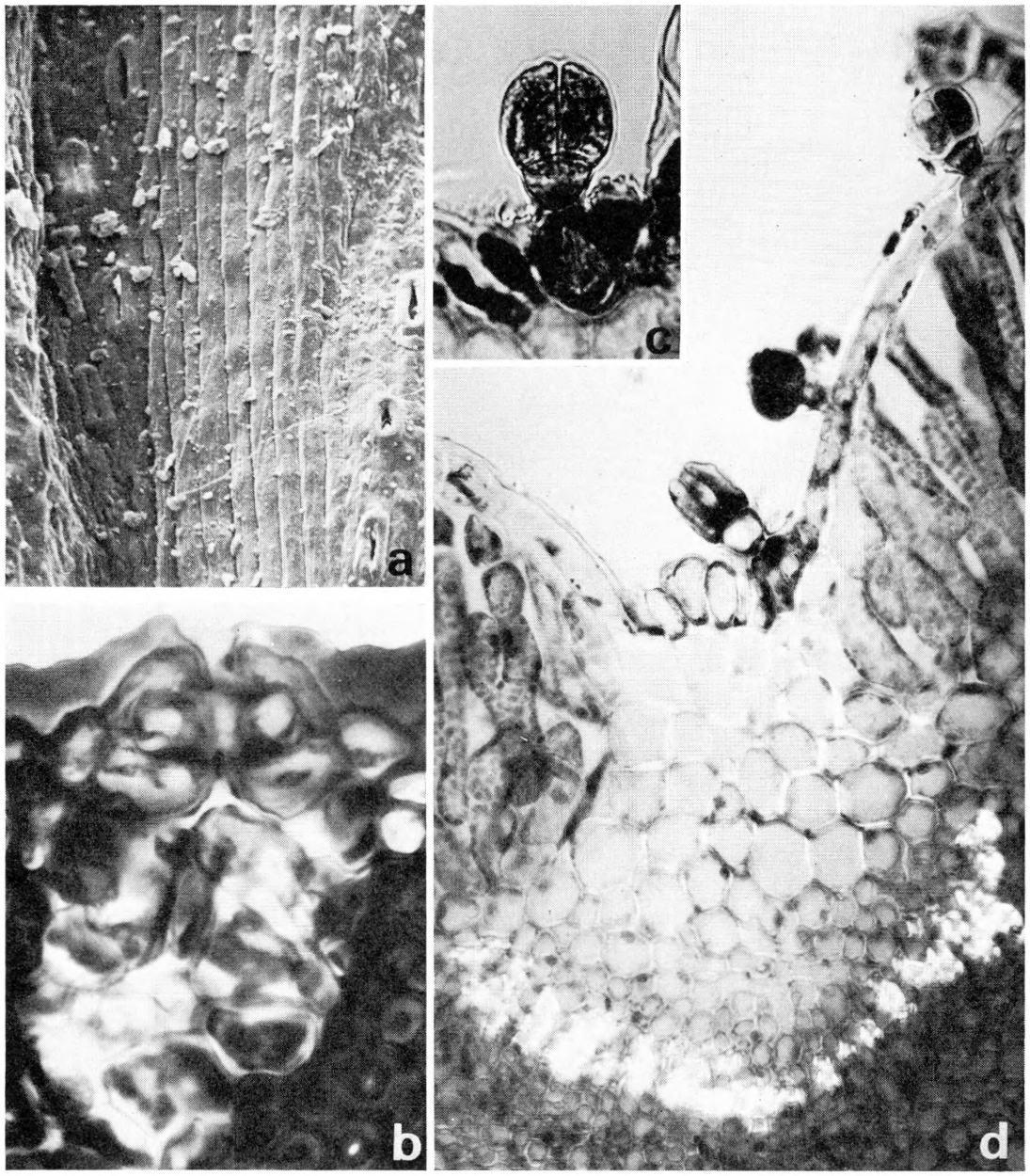


Fig. 46. *Diostea juncea*. a. SEM micrograph of surface; some of the stomata in the groove appear to be closed (× 200). — b. Cross section of closed stomatal pore and substomatal cavity; the latter filled with parenchymatous suberized cells (× 800). — c. Glandular hair from groove above middle vein in leaf (× 400). — d. Transection of leaf at groove and middle vein, parenchyma between xylem (showing up) and small upright thin-walled cells in groove (× 320).

Indeed, it has green assimilating branches and long internodes, but the opposite, lanceolate, pinnately lobed to coarsely dentate leaves are 1–2.5 cm long and are not always shed early. The stems have two almost opposite grooves which can be followed through the entire internode. The groove starts in the angle where two leaf bases adjoin and ends just above the expanded middle part of the leaf base at the node below. The leaves have short petioles. A groove with many glandular hairs is found above the middle nerve and continues on the adaxial side of the petiole. The margins of the leaf bases and the uppermost broader part of the stem grooves carry some short acute hairs. There are numerous glandular hairs in the stem grooves.

Leaf anatomy

The leaf is dorsiventral, glabrous or has scattered, short papillate hairs. Near the margin on the upper side circular nectaria occur, sometimes several on the same leaf. The nectaria are about 0.5 mm in diameter and placed in a flat depression in the leaf surface (Plate XIXa). They consist of a dense secretory palisade tissue forming a "head" which rests upon two layers of cells with cutinized (suberized?) radial walls. The secretory palisade tissue is covered by a number of thin lamellae which react to Sudan IV and may be a multiple cuticle. In some places these cutinized lamellae form beaked protrusions which at the tips seem to be covered by a single lamella only. Such beaks may be compared with similar structures found e.g. in *Cassia* (p. 24) and are believed to function as openings through which nectar is excreted. The two layers of cells with cutinized radial walls evidently have something to do with the production of nectar. The cutinized walls are rather thick and may be able to serve as pathways for excretions, which flow towards the secretory palisade tissue. In one case an additional palisade layer was inserted in a small part of a nectarium. Below this additional layer were also a few cells in which cutinization of the radial walls was initiated. In the middle of such walls very thin lamellae seem to have been formed on both sides of the middle lamella. The rest of these walls were not stained by Sudan IV. The secretory palisade cells sometimes contain dark substances which are believed to be tannin. The experiences obtained from studies of other nectaria (see pp. 5 and 101) have been considered together with the above mentioned observations and have led to a theory which may explain the peculiar common structural features of nectaria.

Assuming that the basal cells with the cutinized radial walls excrete a concentrated sugar solution, this excreted sugary fluid would probably increase the osmotic pressure in the cells too much unless the fluid was separated from the cells by a cutinized (or suberized) wall lamella. The thick cutinized walls are thought to be built up after repeated excretions.

The sugary fluid may be transported through the walls of the secretory palisade tissue to the surface where it is liberated through the beaked protrusions mentioned above. The walls separating the cells of the head are not cutinized except where they widen near the surface (see Plate XIXb). The above theory therefore must be supplemented with the assumption that the cells in the head have a concentration of cell sap

which is able to resist the influence of the sugary solution passing through the walls to such a degree that the protoplasts do not shrink. On the other hand they may secrete a sap which dilutes the more concentrated solution produced by the basal cells. These have clearly larger vacuoles than the majority of cells in the palisade layer of the head.

In the groove above the middle vein of the leaf there are many glandular hairs as well as some upright cells rich in cytoplasma and without detectable cuticle (Fig. 46c, d). These cells rest upon large parenchyma cells which again cover a tissue of small cells on the dorsal side of the xylem in the bundle below. It is impossible to determine whether the parenchyma between the xylem and the glands and the upright epidermis cells leads water from the bundle to the surface or vice versa; but we are more inclined to assume that water which assembles in the furrows is absorbed and conducted through the parenchyma to the vessels. Another possibility might be that the glands are excretory and the small upright cells water absorbing. Glandular hairs of the same type as those found on the leaves are abundant in the grooves on the stem where they usually protrude their heads, while the stalk cells become embedded in the thick cuticular layer of the surrounding epidermis cells. Obviously the glands produce some kind of sticky substance to which groups of small fungal cells adhere. However, water which seeps down in the groove will reach the cells in the heads and may be absorbed. Undoubtedly these observations call for experiments e.g. with supply of Neutral-red solutions to the grooves.

Outline of stem anatomy

Troncoso (1957, fig. 2 and p. 170) has studied the stem anatomy. She pictures 27 large and small fiber strands uniformly scattered along the periphery of the stem. Inside the chlorenchyma of the cortex 19 phloem fiber areas are found just outside a continuous cylinder of phloem and xylem which surrounds the pith.

To this information given by Troncoso we may add that the peripheral fiber strands are separated from the epidermis by roundish collenchymatous cells (Fig. 47b). Somewhat similar round cells occur also in a layer which like an endodermis forms a sheath covering the fiber strands on both sides. On the adaxial side of the fibers the cells of this sheath come very close to one another before they diverge and continue in a cylindrical layer which has a position corresponding to an endodermis. Although not very conspicuous, we believe that in this species an endodermis can be traced and that it bulges out and surrounds the fiber strands. This means that the peripheral fiber strands as well as the fiber areas near the phloem are perivascular.

Occasionally phellem cells are formed near one of the peripheral fiber strands. The cells seem to form a lenticel-like area (cp. *Fabiana* p. 57), or they may initiate a localized periderm which cuts off a small part including a fiber strand thereby contributing to an increase in the girth of the stem.

The xylem is diffusely porous or almost ring-porous and the rays are 1(-2) seriate. A medullary sheath of cells with rather thick walls is intimated and sometimes the pith contains a central group of cells with thick walls.

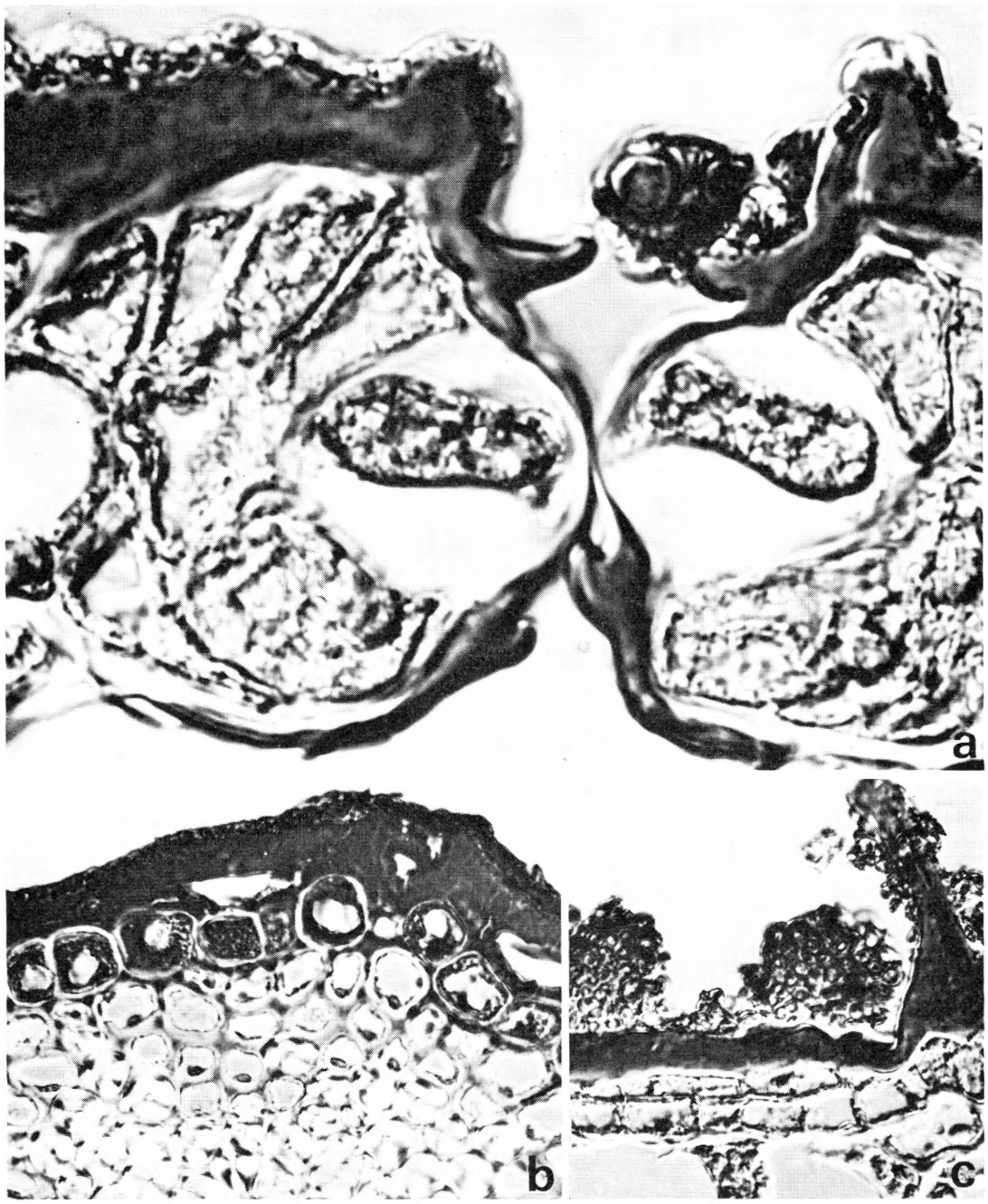


Fig. 47. *Diostea juncea*. a. Cross section of asymmetrical stomatal opening. Fungal cells inside outer front cavity (Sudan IV staining and interference contrast, × 2000). — b. Cross section of stem. Outer part of cuticular layer peeling off; irregular refractive whitish bodies in the epidermis cells. — c. Multiple epidermis formed below groove, groups of fungal cells outside cuticular layer and adhering to cutinized hair base (Sudan IV staining, × 500).

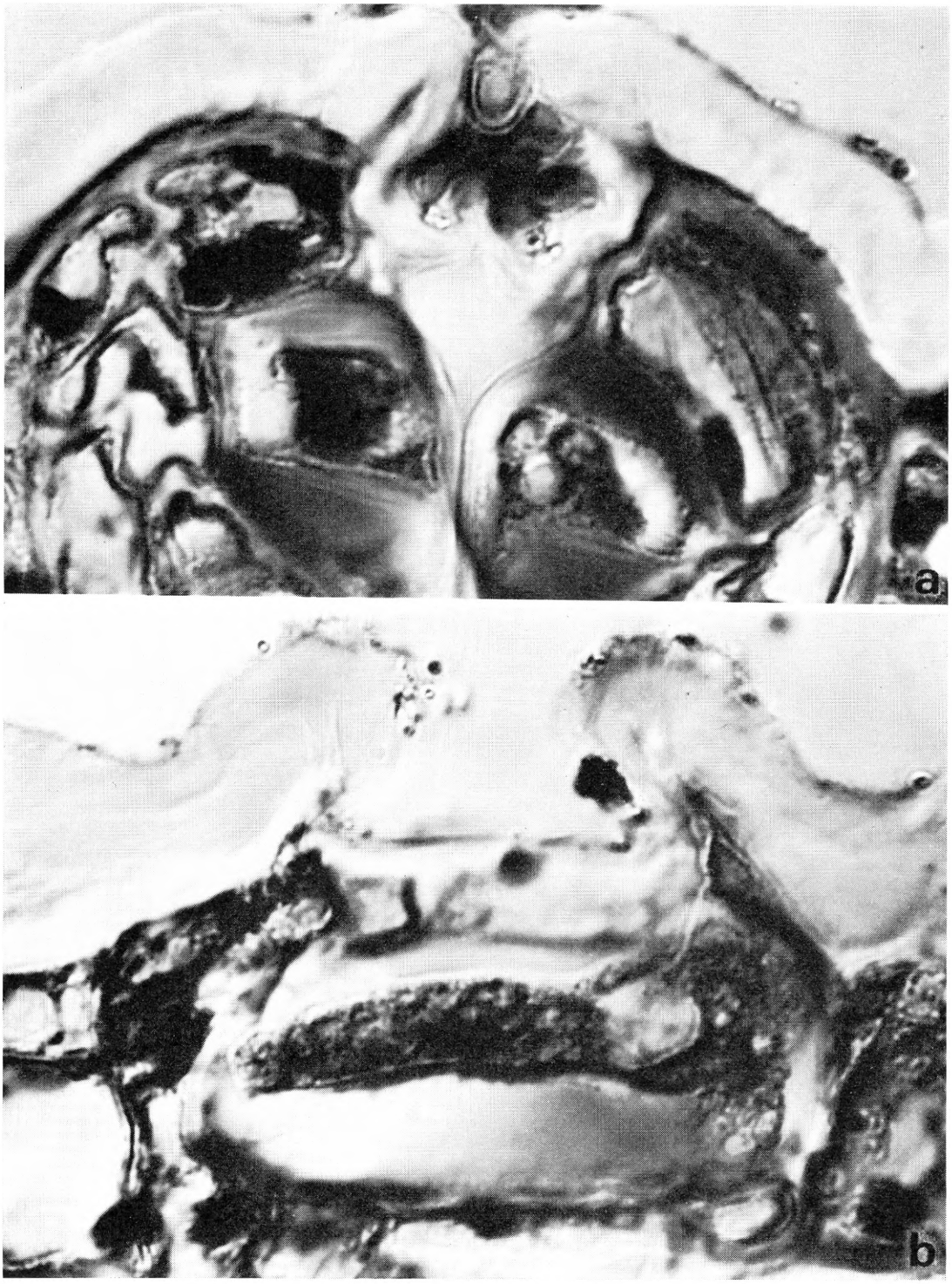


Fig. 48. *Diostea juncea.* Stomatal apparatus in cross section (a) and longisection (b). Fungal cells in outer front cavity in (a). The overarching subsidiary cells produce a projecting rampart surrounding the outer front cavity. Delicate channels radiate into the rampart. Refractive bodies in protoplasts (Quadruple staining, interference contrast, × 2000).

Epidermis

Outside the peripheral fiber strands the epidermis is unilayered, but in the areas in between and in the furrows it is very frequently multiple with 2–3 cell layers (Fig. 47c). The outer cells are covered by a 10–15μ thick cuticular layer and the radial walls have cuticular flanges in their outer part. New cuticular layers are formed from below and the older, outer layers peel off (Fig. 47b). This peeling frequently takes place outside the peripheral fibers (Plate XIXc).

Scattered cutinized hairs are found in the furrows (Fig. 47c) and glandular hairs are sometimes abundant here (see above) together with clumps of small fungal cells (Fig. 47c).

The outer epidermal cells are brownish due to contents of tannin vacuoles. In the center these cells usually contain a roundish, polygonal, or irregular whitish area, which may represent a tannin-free part of the vacuole (Fig. 47b, Plate XIXc). The same whitish areas occur in the cytoplasm of the guard cells (Fig. 48b), cp. further p. 30.

The stomatal complex is interesting because of the big size of the guard cells, the ledges, and the many subsidiary cells. When viewed from outside the stomatal pores project as elongate chimneylike bodies (Fig. 46a, Plate XIX). In side view the projections are 15μ high. The long axis is almost parallel to the axis of the stem (Fig. 46a). The opening into the front cavity may be 20–30μ long and 5–20μ broad.

From transections of the stomatal pore it appears that there are two front cavities, an outer one inside an oval or oblong projecting rampart formed by overarching subsidiary cells, and an interior front cavity inside and below the outer ledges and above the central pore. The overarching subsidiary cells send out micro-channels into the rampart (Fig. 48a, b). Fungal cells are frequently found in the outer cavity (Figs. 47a and 48a). Very rarely do they penetrate into the interior front cavity and only in a few exceptional cases may they infect the plant.

Inside the central pore a back cavity is found between the pore and the inner ledges which probably are formed by two epidermis cells placed below the guard cells and behaving as guard cells imitators. The ledges are frequently placed symmetrically in relation to a plane through the pore. However, it may be common to find the ledges asymmetrically arranged (Figs. 47a, 49b). In such cases the pore seems to be zigzag-shaped. It is worth emphasizing that the opposite sides of the pore are different along the entire stretch from the rampart to the substomatal chamber. The asymmetry is not a result of any dislocation of the guard cells, e.g. a result of the microtome technique.

The outer and inner walls of the guard cells are as usual very thick, but the walls facing the pore also thicken. However, frequently a narrow part is maintained in the same area where the cuticular layer is reduced to the normal thickness of a cuticle (see Fig. 49).

The cells which imitate the guard cells have much thinner walls. However, during the development these cells also grow and their walls thicken. They approach one

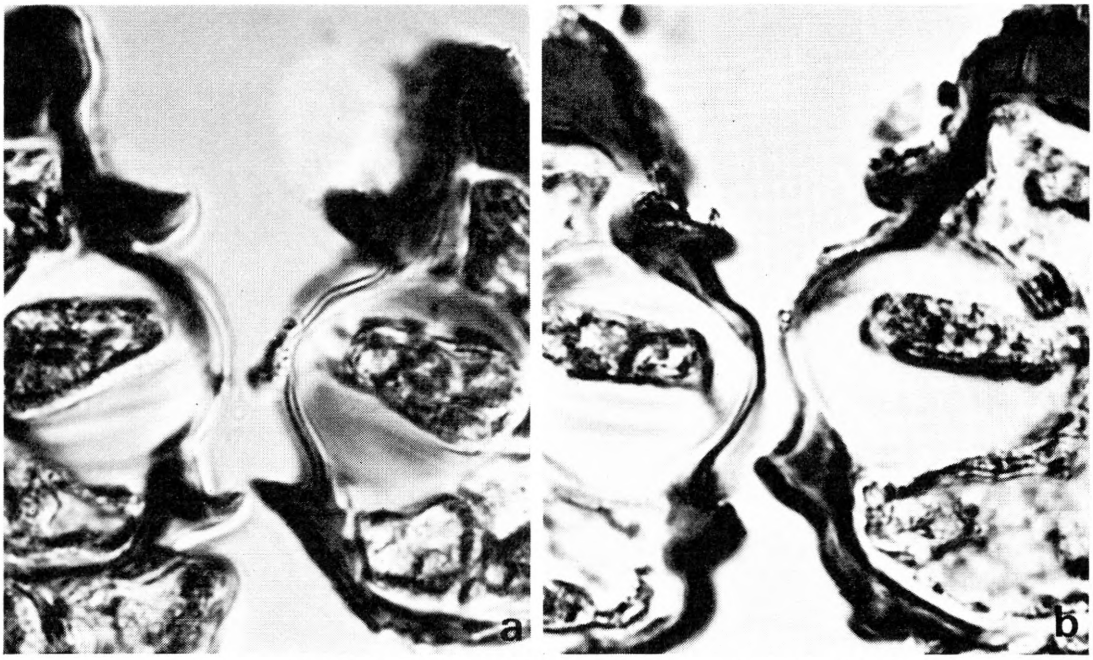


Fig. 49. *Diostea juncea*. Two stomatal pores, that on the right (b) asymmetrical (Sudan IV staining, interference contrast, ×1600).

another very much and seem to contribute to a closing of the pore. This happens almost at the same time as the genuine guard cells become inactive due to wall thickening. This closure is followed by a filling up of the substomatal chambers with parenchymatous cells which finally get suberized walls and die (Fig. 45b). This type of development seems to take place where stomata are placed near fiber strands.

The number of subsidiary cells is great. They are arranged in rings around the stoma. Sometimes these cells contain more than one nucleus. If the cells beneath the guard cells are included, the total number may exceed 30. On the left side of the pore in Fig. 47a there are 9 cells arranged in a semicircle. One or two cells lie along the backside of the guard cells where the walls are thinnest and may bulge at high turgor.

4. Species with furrowed stems. All stomata placed in furrows, cortex chlorenchyma arranged inside and on both sides of the furrows. Fiber strands or sclerenchymatous bands in the middle of the ridges reaching the peripheral layers.

Although evidently connected with the preceeding group with more or less angular stems and ribs, the species which belong to the following group have clearly reached a much more advanced stage characterized by furrows that probably act as huge

sheltered extra front cavities common to a great number of stomata. This subtype of the stem-assimilatory life form occurs in a number of different families e.g. *Casuarinaceae, Fabaceae, Celastraceae, Verbenaceae,* and *Asteraceae.* Important taxa having this structure are e.g. *Corallospartium crassicaule* (Slade 1952), *Retama raetam* (Evenari 1938), *Neosparton* (Troncoso 1957), *Aylacophora deserticola,* and *Nardophyllum bracteolatum* (Cabrera 1953, Solbrig 1961).

Neosparton aphyllum (Gill. et Hook.) O. Ktze.

Material: Mendoza Prov. W. Argentina: Atuel area near Laguna Blanca, 1600 m. above sea level, Böcher, Hjerting & Rahn No. 741, Nov. 2, 1955, 5 km west of El Sosneado, 1500 m. above sea level, Böcher, Hjerting & Rahn No. 909, Nov. 10, 1955, and El Sosneado, 1600 m., Böcher, Hjerting & Rahn No. 1460, Dec. 25, 1955.

Occurrence and morphology

Neosparton aphyllum occurs mainly in western Argentina in the northern part of the Patagonian steppe province (Troncoso 1957, fig. 1). It is very abundant in the shrub steppe and grows frequently in loose sand e.g. at the entrance to the Atuel Valley (Böcher, Hjerting & Rahn 1972, Table 5 and 9).

It is a 1–2 m. tall shrub with many opposite branches. After blooming the growth

Fig. 50. Flowering *Neosparton aphyllum* in the Patagonian steppe vegetation near Estancia El Sosneado, Mendoza prov. W. Argentina.

of the terminal shoot ceases after which two opposite buds below develop into new branches. Thus the shoot structure becomes sympodial. (TRONCOSO l.c. fig. 12 and our Fig. 50).

The stems have 20–24 (17–28) furrows and carry rudimentary scale leaves only. In the floral region the small leaf blades may sometimes remain, but usually they are shed early leaving leaf bases which terminate in scars. The morphological upper side of the leaf base carries many hairs as does the stem in the axil. Occasionally some resinous brownish-yellow substance gathers in the axils or is found as a cover on top of the leaf base scars. Axillary buds may also be resinous. The surface of the stems is covered by short hairs in the floral region but is otherwise glabrous apart from the furrows.

Outline of stem anatomy

The anatomy was first studied by TRONCOSO (1957 fig. 14). A cross section of the stem shows 20 furrows in which stomata and glandular hairs are found on the bottom. The outer part of the furrow has many cutinized hairs which form a cover over the bottom area with the stomatal openings. A hypodermis is present in most parts of the ridges (Fig. 52b, 54b). Its cells become more or less collenchymatous. The ridges have a central strong fiber strand. Other fibers are found outside the primary phloem. Chlorenchyma occurs in the areas between the fibers in the ridges and the furrows, and beneath the bottom of the latter, where also a number of sclereids are found as idioblasts or in groups of a few cells. At an early stage a continuous cambium ring is formed so that the wide pith becomes surrounded entirely by xylem and phloem. The pith consists of large parenchymatous cells with rather thin walls.

Epidermis

Cuticular layer and cuticle

The cuticular layer varies in thickness, always being very thick on the ridges. This is the case already in young stems where the layer may be 4–8μ thick (Fig. 51a), while in older stems the thickness may vary between 8 and 21μ. In cross sections of the ridges one may see two or three areas where the cuticular layer is particularly thick (Fig. 54a). These areas correspond to the low swellings which are conspicuous on the surface of the ridges when observed in the SEM (Plate XXa, b). In the furrows the cuticular layer may not exceed 2–3μ in thickness (Fig. 54c). The cuticular layer stains intensely red with Sudan IV. In polarized light it is completely dark in young stems, but in older ones with a very thick cuticular layer small areas just outside the middle part of the epidermal cells show up, while the intervals off the radial walls remain dark. The birefringent spots may be due to wax secreted by the cells (cp. further discussion on p. 125).

The pattern of longitudinal and transversal cracks which is seen in dry specimens on SEM micrographs (Plate XXb) is sometimes very uniform. The cracks are

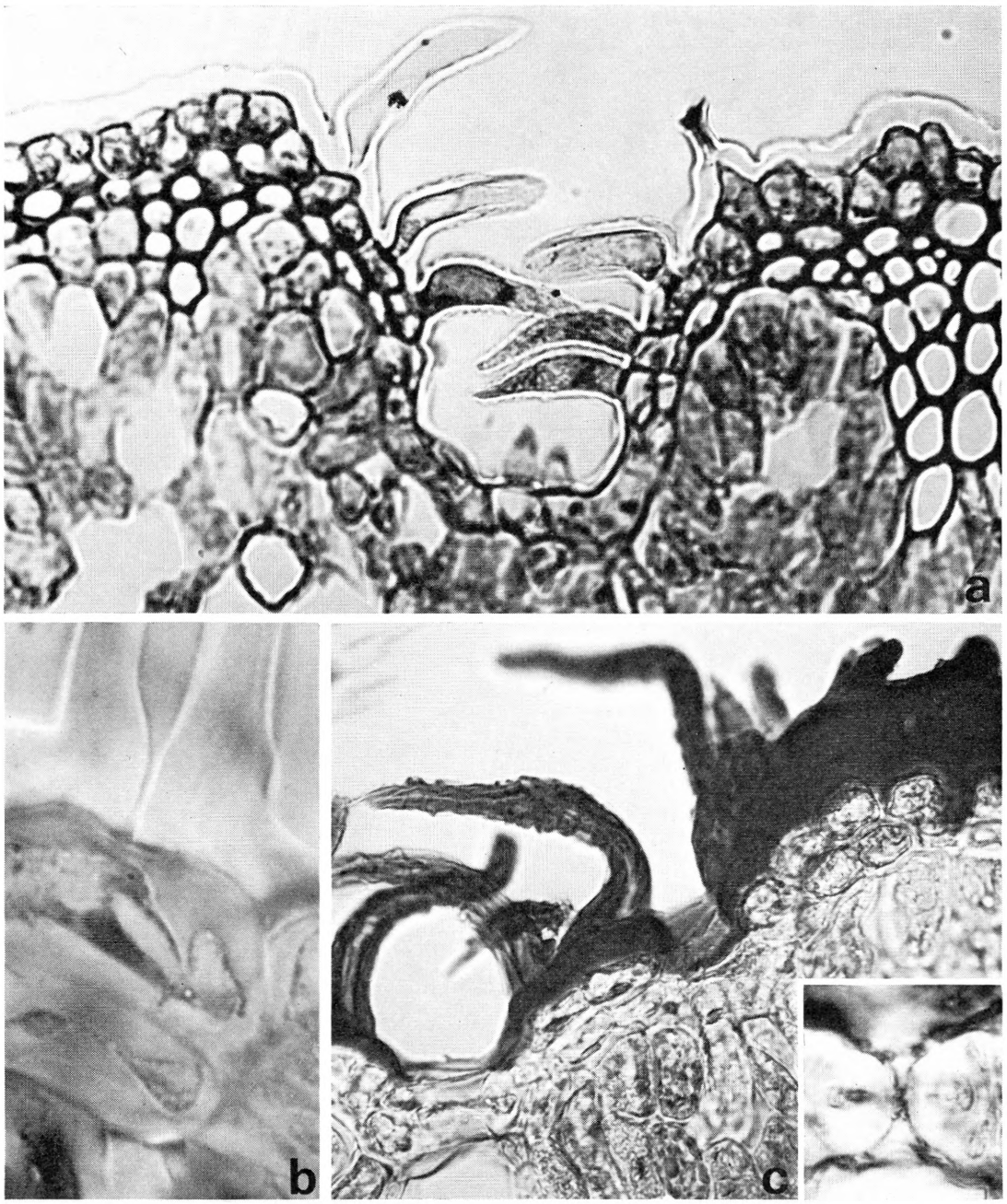


Fig. 51. *Neosparton aphyllum*. a. Cross section of furrow in young stem. Hairs in furrow still living (dark spots nuclei), those at the margin of the furrow dead (on the right, base of dead glandular hair). On the right, young fiber cells in stage of wall development (Quadruple staining, × 500). — b. Hair base showing empty narrow channel replacing former plasmatic connecting strand (Safranin-Fast green, semipolarized light, × 2000). — c. Side of furrow in older stem. Two stomatal openings and very thick cuticular layer. In corner, cross section of stomatal opening with small projections which gear into one another (Sudan IV staining, × 500 and (corner) ×800).

more numerous near the furrows and less so on the top of the swellings. In alcohol fixed material it is possible to find cracks in the cuticle some of which go somewhat deeper into the cuticular layer (Fig. 54b). In many cases the distances between the cracks in the cuticle are almost of equal size and may correspond to those found on the SEM micrographs and also to the diameter of one or sometimes two epidermal cells. The cracks may be formed outside anticlinal walls, but they never reach deeply into the cuticular layer. New epidermal cells which during the growth are inserted between the old ones may, therefore, at the same time as they are formed also contribute to the growth of the cuticular layer. Accordingly, new material may sometimes be deposited without any observable change in the structure of the common cuticular layer.

Trichomes

Three types of trichomes are found in or in close connection with the furrows: (1) Simple, unicellular hairs which die and become airfilled. (2) Glandular hairs. (3) Large, peltate glands with a secreting palisade tissue.

The simple hairs are developed in great number as single elongate cells in continuation of epidermis cells placed near the entrance to the furrows and in their outer part. From the beginning their walls are rather thick and the cuticle has small elongate protrusions. The hairs are narrower at the base and sometimes contain two nuclei. Those placed inside the furrow keep alive longer (Fig. 51a). Before the hair cells die, the walls have become thicker and are cutinized. At the base they may keep a narrow connection with the underlying epidermis cell for some time (Fig. 51b), but finally this cell produces a thick cuticular layer between the dead hair cell and the living epidermis cell (Fig. 51c, Plate XXd).

The hairs are usually bent so that they form a roof over the bottom of the furrow. The outermost hairs on both sides of the entrance are short and resemble acute warts. Longer hairs placed in this position are shed. Just inside the entrance follow a number of flattened scale-like hairs (Fig. 51a) on which the small elongate protrusions form a curious pattern (Plate XXc).

The glandular hairs occur in or near the bottom of the furrows. They have a unicellular stipe and a pluricellular head, which is globular (Fig. 52b, Plate XXd), or sometimes with an irregular somewhat lobed surface (Plate XXIa).

Nothing is known about the secretory activity of these typical glandular hairs, but they have an interesting position and may contribute to reduce the transpiration through the stomatal openings. In *N. ephedroides* they are more numerous. In *N. aphyllum* they may to some extent be replaced by larger glands and transitional trichomes. In a longisection of a furrow a row of 300 epidermal cells were investigated. Most of the cells carried simple hairs, six had typical glandular hairs while two larger glands were inserted between the normal epidermis cells (cf. Fig. 53d).

The larger glands have a multicellular stipe and a head in which the uppermost part is occupied by a secretory palisade tissue. A striking feature is that such glands

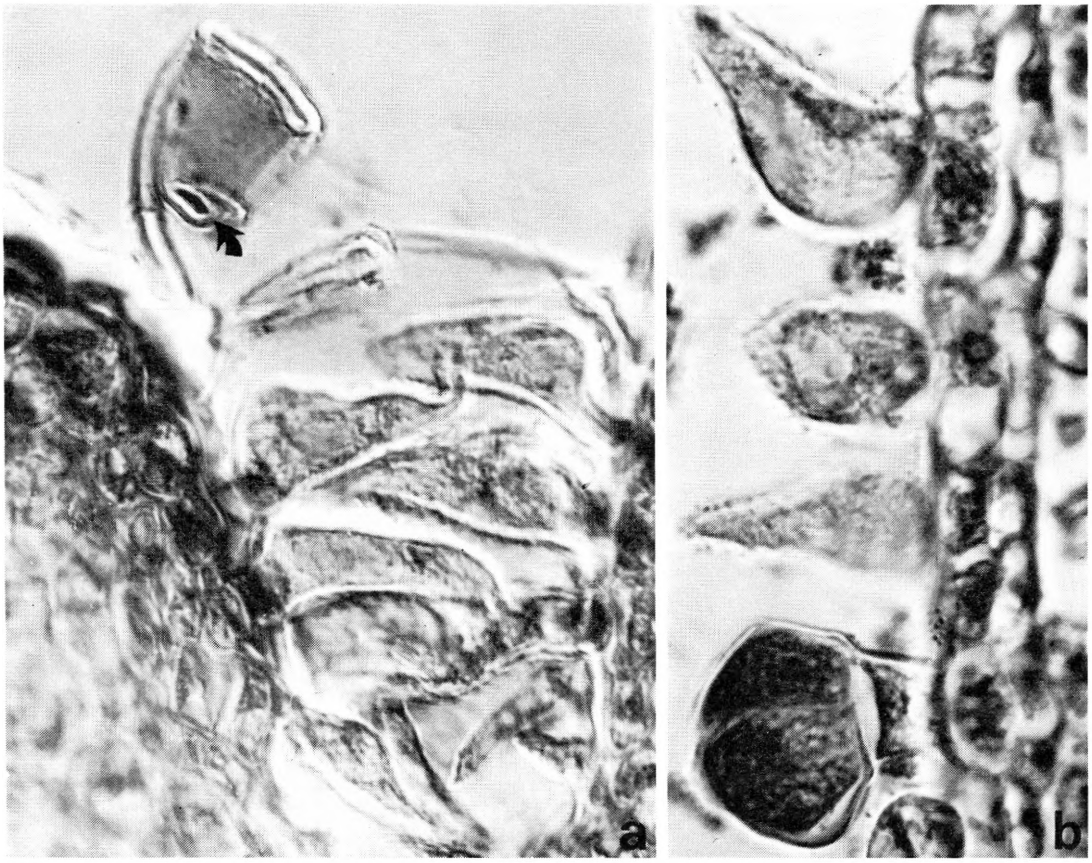


Fig. 52. *Neosparton aphyllum*. a. Cross section of furrow in young stem showing cogwheel-like hair pattern. Uppermost flat hair is bent, the arrow points towards the tip. — b. Longisection of similar furrow. One glandular hair and three non-glandular, that in the middle cut across. A hypodermis is developed (Safranin-Fast green, × 800).

appear "rooted". Some ± elongate cortex cells are connected with the stipe cells or contribute in their distal part to the formation of the stipe (Fig. 53c, Plate XXIb).

In the center of the stipe the radial cell walls are thick and cutinized (Fig. 53e). Similar thick cutinized walls may be found centrally in the lower cell layer in the head but seem rarely to extend to the upper palisade secretory tissue (Plate XXIb). In some cases cutinization of parts of the tangential wall between the head and the stipe was observed (Fig. 53d). The cuticular layer of the surrounding epidermal cells continues outside the stipe region but the head has only a thin cuticle.

The glandular heads vary in diameter from 67 to 127μ. In the widest glands the stipes were usually broad but sometimes hardly developed. In transection they had about 12–26 secretory cells of which the peripheral ones might be curved like bananas (Plate XXIb on the right).

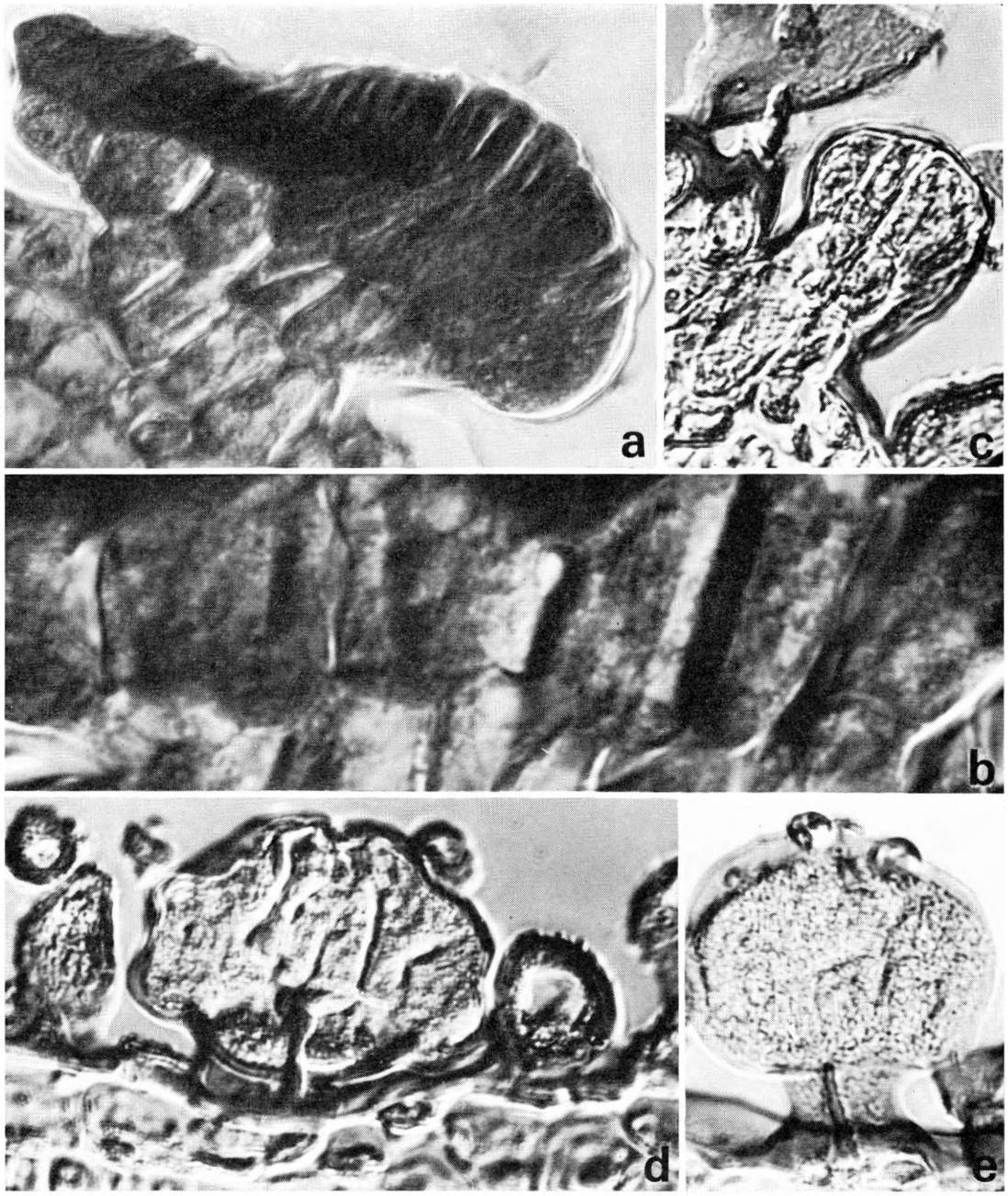


Fig. 53. *Neosparton aphyllum*. Extra-floral nectaria (glands) all situated near entrances to furrows. — a. Larger nectarium with many narrow secretory palisade cells situated on broader basal cells with cutinized radial walls and below, several cells forming a "root". Cuticular bladders on surface (Safranin-Fast green, × 800). — b. Basal cells from (a) with thick radial walls (× 2000). — c–e. Three smaller glands showing cutinization of radial walls, in (d) also of basal wall, in (c) many cells forming "root" (Sudan IV staining, × 800).

The cell layer beneath the palisade tissue may be of particular interest. As mentioned on p. 91 the median radial walls and sometimes most radial walls stain with Sudan IV and are particularly thick. The nuclei in the cells are very big suggesting secretory activity. In some cases intercellular spaces were detected in these walls. The largest gland found had eight cells under the palisade head (Fig. 53a), and all seven walls between these cells had a narrow cavity which appeared to be lined by a very thin, dark, and possibly cutinized or suberized layer (Fig. 53b). Even in the stipe small intercellular spaces occur in the walls. The narrow cavities seemed to continue in between the cells in the upper palisade layer and might terminate in minute pores occuring very near the surface of the gland but below the cuticle. In many cases the latter was raised in small bladders outside such pores (Plate XXI).

The transitional glandular trichomes may have two or very few stipe cells or one club-shaped stipe cell with a big nucleus (Plate XXIa) and with a head of usually four parallel cells which taper into a "beak". The secretion collects beneath the cuticle outside the central wall which seems to contain a narrow intercellular duct. In one case a transitional trichome had one large stipe cell and a head of eight parallel cells.

With increasing age transitional trichomes placed near the entrance to the furrow are cut off by the thick cuticular layer which is produced by the underlying cell. A similar fate is probably shared by the larger peltate glands. Here, however, it is not quite clear how the broad stipe behaves. In all probability the whole gland with its stipe wilts and is shed, while the cells below which form a rooty structure produce a cuticular coating which later is difficult to distinguish from the cuticular layer of the adjacent epidermis cells.

The larger glands are always placed on the border of a furrow or at the entrance to it. They were not observed in older parts, but may be rather numerous in young twigs. When observed with low magnification from the outside they appear as yellowish, shiny, globular bodies. In alcohol-fixed material the secreted matter is mostly dissolved, but in some cases some yellowish droplets occurred seemingly beneath an expanded cuticle (Fig. 53e).

The glands found in *Neosparton aphyllum* are clearly related to the peltate glands of *Clerodendron trichotomum* described by Dop & Dufas (1928, fig. 2). In *Clerodendron fragrans* Reinke (1876) describes extrafloral nectaries with a secretory palisade tissue, but these glands are completely sessile and much broader.

There is also much resemblance to the peltate glands of the *Lamiaceae*. Klug (1926) found that the secretion here was preceeded by a peculiar fold of the cuticle in which the first secretion was accumulated. In *Neosparton* a number of such folds were particularly clear in the case pictured in Plate XXIc, in other cases the cuticle was raised in the form of a bladder although in some of the broadest glands the bladder was localized involving only minor parts of the secretory surface.

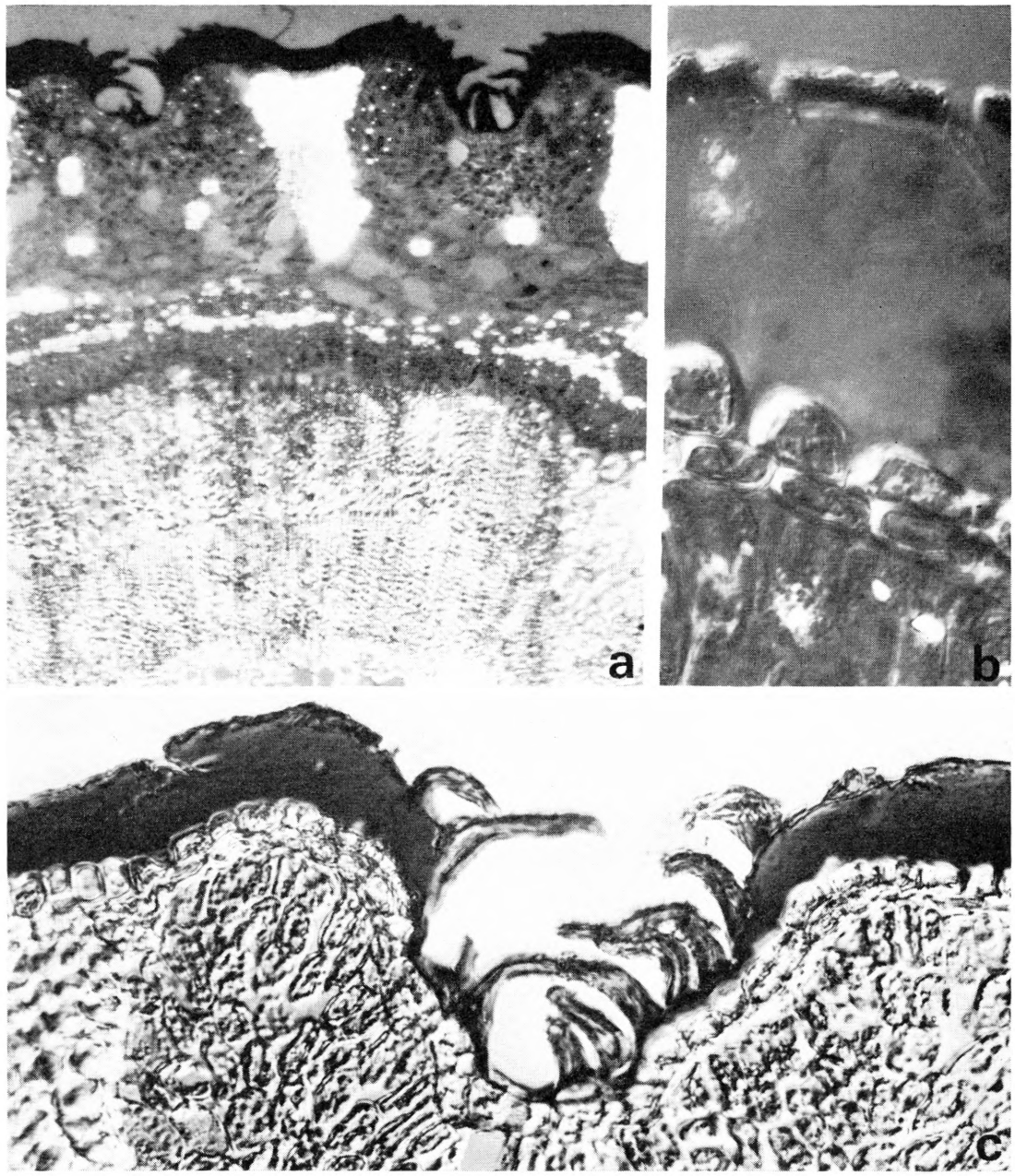


Fig. 54. *Neosparton aphyllum*. a. Cross section of stem in polarized light. Fiber strands, cortical sclereids, phloem fibers and sclereids as well as xylem showing up (Sudan IV staining, × 80). — b. Cuticular layer with cracks in outermost part, epidermis and hypodermis (Safranin-Fast green, interference contrast, × 2000). — c. Cross section of furrow in older stem (Sudan IV staining, interference contrast, × 500).

Stomata

Stomata are placed in or near the bottoms of the furrows. They are very slightly sunken below the surface. The guard cells are provided with low outer and inner ledges. Their walls are thick and have a clear lamination which indicates that the protoplasts off the center of the stoma with increasing age withdraws from the pore. At the mature stage of the stoma the closing seems to be particularly effective by the formation of a number of very small elongate cutinized projections, which like cogs in a cogwheel fit into one another (Fig. 51 c, Plate XX e).

Cortex

The cortex consists of large fiber strands in the ridges and chlorenchyma which contains sclereids. In young stems the walls of the fiber cells are not very thick (Fig. 51 a), but soon their lumen becomes narrow. The chlorenchyma is denser towards the outer part of the ridges, while near the stomata it is looser with many substomatal chambers and other spaces between rows of green elongate cells which near the surface resemble leaf-palisade cells. The sclereids are circular in transections with a very clear lamination (Fig. 55 c). In longisections they are elongate and appear frequently to be placed in rows.

Stele

A striking difference is observed between young and old stems. Young stems have a vascular cylinder consisting of smaller and larger vascular bundles connected by short interfascicular regions. At a time when the photosynthetic tissues in the cortex are rapidly developing and active and the simple hairs in the stomatal furrows still have nuclei, the vascular system is far from being mature. The primary phloem is well developed, but the xylem consists of a narrow zone of metaxylem cells which connect the protoxylem groups in the bundle areas (Fig. 55 a). No fibers are visible. On the border between the cortex and the primary phloem a cell row is found which, although being without Casparian strips, probably corresponds to an endodermis (Fig. 55 a, arrow). Just inside this layer and particularly on the outside of the primary phloem some cells with small diameters occur in connection with some cavities. At first these cavities were thought to be artefacts, but a closer study including the older stems made it evident that they constitute lysigenous spaces in which phloem fibers and sclereids develop later. The small cells inside the layer which was believed to be an endodermis have the position and properties of a pericycle and they seem to multiply and develop into fiber strands and sclereids.

However, a similar process seems to take place in the area where the metaxylem develops and the cambium is formed. In the young stem there is here a row of roundish or angular lysigenous spaces. They are placed exactly where a system of elongate sclerenchymatous cells later develop. In the transections of older stems these cells form a layer which is 1–3(4) cells broad and not continuous (Fig. 55 b). From observations of radial sections it becomes evident that the elongate sclerenchymatous cells

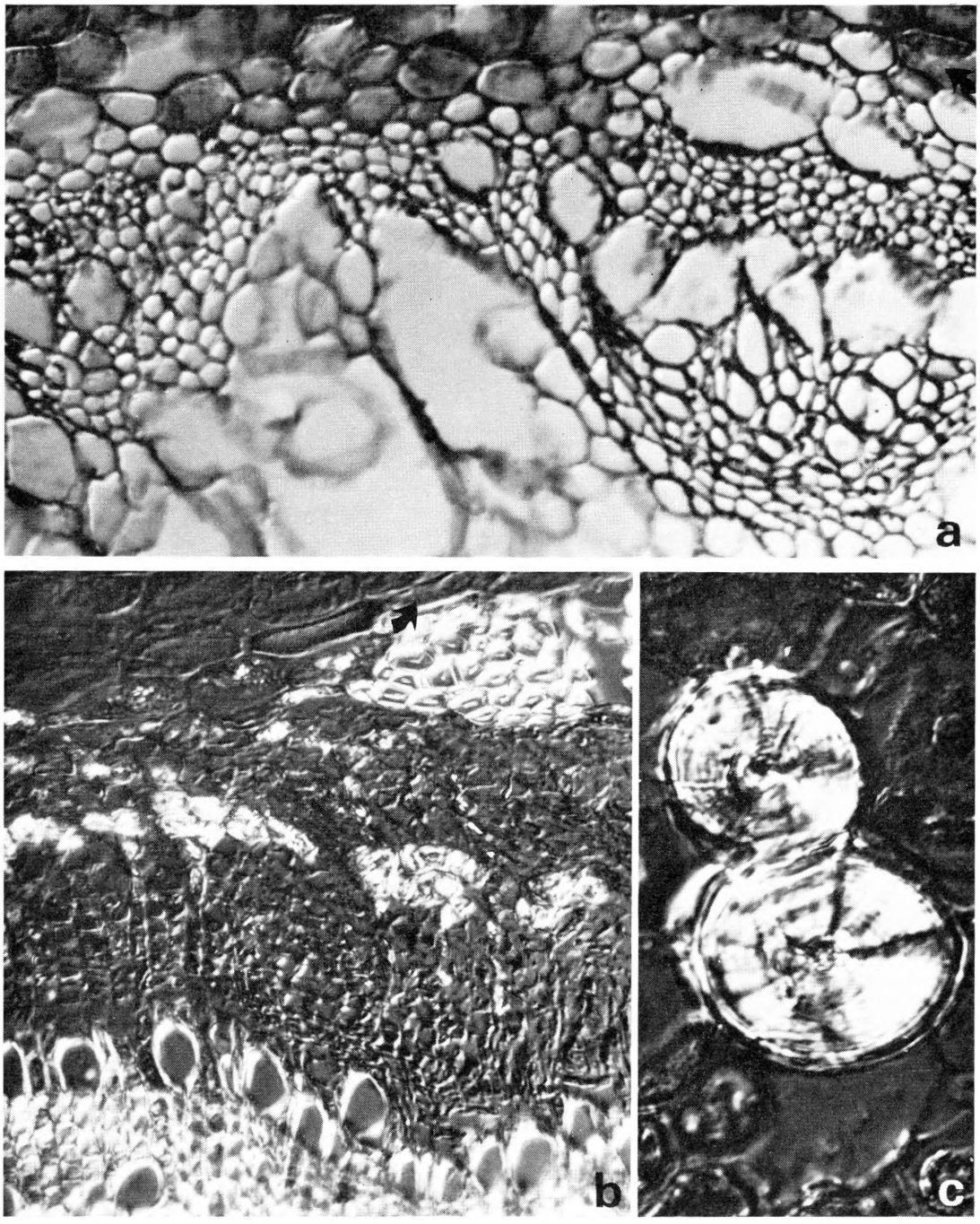


Fig. 55. *Neosparton aphyllum*. a. Cross section of young stem. Arrow pointing towards endodermis. Cavities replacing protophloem and furthermore developed between the primary and secondary phloem and the xylem (× 320). — b. Later stage as (a) fibers replacing cavities in young stem (polarized light, × 500). — c. Cortical sclereids, cross section (polarized light, × 800).

are placed in radial rows which probably are formed by the cambium at the transition between the primary and the secondary phloem. Some of the cells are tapering in one end and are clearly terminal cells in strands of cells formed by transverse divisions of fusiform initials. The initials seem to have formed radial series. At any rate, the upper and lower walls in the sclerenchymatous cells are on the same level and the tissue stratified, a fact which is in accordance with the wood structure which appears to be storied although not so uniformly as in *Neosparton ephedroides*.

Another feature of interest is the occurrence of small narrow rectangular crystals. In the photosynthetic parenchymatous cells they occur mostly singly. The green cells form rows of cells which run towards the endodermal layer. In our material the cells in this layer have almost without exception an assemblage of crystals of the same size and shape, thus indicating some kind of physiological connection. However, there are also a number of phloem parenchyma cells with similar gatherings of these crystals.

The supply of water to the photosynthetic tissues and the conduction of carbohydrates from the green cells to the phloem seem to be easy. The distance is short and the sclerenchymatous layer is interrupted by rays. As already mentioned it is more difficult to understand how the cells receive sufficient water during the first stages of the stem development. However, some transpost may possibly take place in the immature cortex fibers (cp. Fig. 51 a and discussion in Mitchell & Worley (1964)).

The first annual ring in the xylem has comparatively few vessels, while in the second and third there are many vessels distributed throughout the growth layer except in the late wood. The rays are uniseriate.

Increase in girth

When comparing the furrows in young and older stems it is evident that the entrances of the furrows with increasing age and diameter of the stem get wider and the sides less steep (Fig. 51 a, c). The number of epidermal and cortex cells increases, while the cells which were supposed to be endodermal are stretched tangentially.

In rare cases the number of furrows may increase slightly. We have not been able to find a series of stages which would prove such a development, but we have seen a great variation in the breadth of the ridges, and in a few cases there were two fiber wedges in one of the broadest ridges. Between the two fiber strands the ground parenchyma reached the epidermis which here had many narrow and young cells inserted between the older ones. Outside the central area of parenchyma the cuticular layer had a few deep cracks. The possibility exists that the epidermal cells outside such parenchyma areas might grow inwards and together with the parenchyma cells produce a fold and finally a furrow.

Neosparton ephedroides Gris.

Material: Near Rio Grande in tributary valley at Ruta 40 (km 388). W. Argentina, Mendoza Province. Böcher, Hjerting & Rahn No. 1858, Dec. 21, 1955, cp. Fig. 56a.

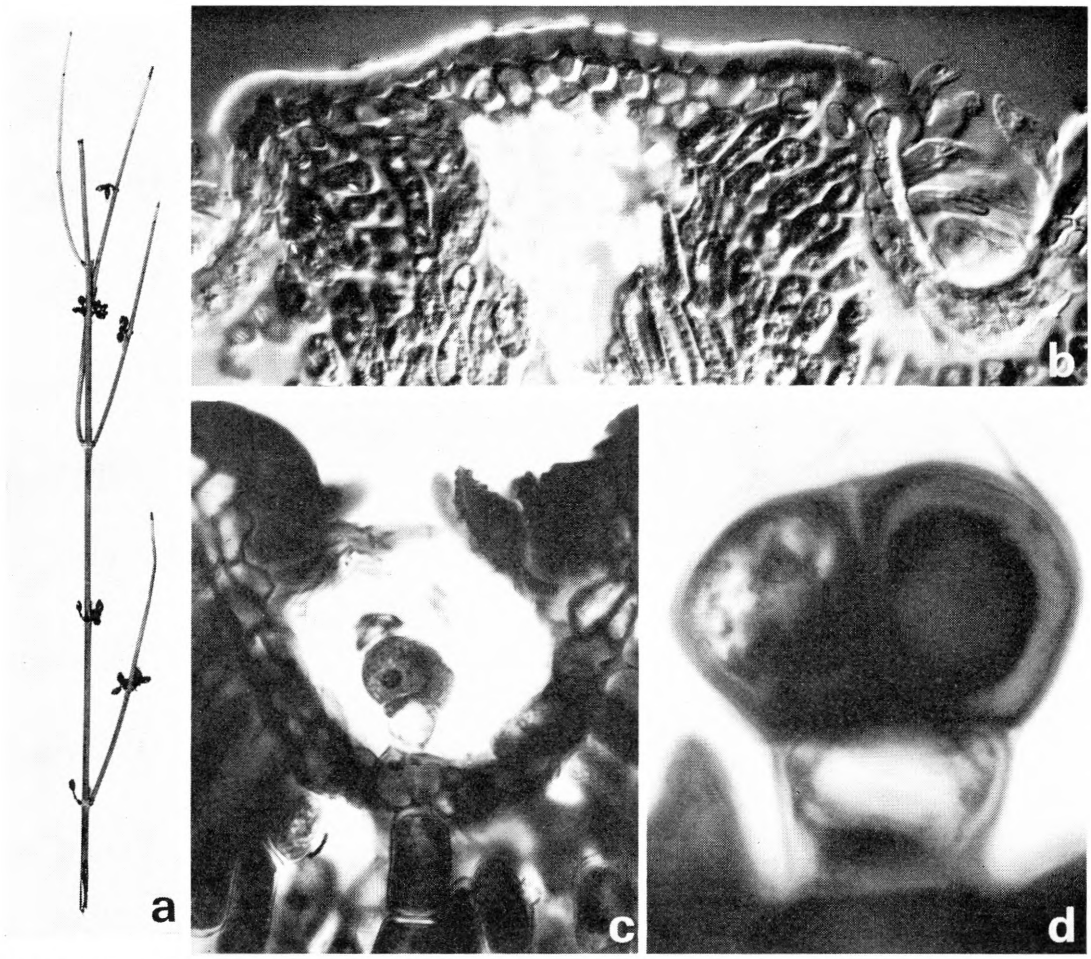


Fig. 56. *Neosparton ephedroides*. a. Part of specimen from tributary valley near Rio Grande. — b. Ridge and furrow; cuticle and interior wall layers of outer epidermis walls showing up as does the central triangular fiber strand (interference contrast, × 320). — c. Cross section of furrow, with glandular hair and dense cutinized hair rows on the border between the thick cuticular covering of the ridges and the thinner one in the furrows. The gland has excreted a substance which is not dissolved during the treatments. A row of green palisade cells below the gland may function as a supply line (Quadruple staining, × 500). — c. Glandular hair with distented cuticle (× 2000).

Occurrence and morphology

According to Troncoso (1957 fig. 1) *N. ephedroides* has a peculiarly disrupted range. It occurs in three areas: (1) Salta, Tucumán and Catamarca in Northern Argentina, (2) the Mendoza province in Western Argentina, (3) Chile at Antofagasta. Cabrera (1958) mentions *N. ephedroides* as a member of the Argentinian Puña vegetation. It grows mostly in sandy soil and ascends to 2400 m. above sea level in Dep. Tinogasta (Catamarca) and to 12–1500 m. at S. Rafael (Mendoza).

The absence from the provinces La Rioja, San Juan and the northern part of the Mendoza province is probably due to climatic factors. These provinces seem to constitute the driest part of the higher elevated areas in Western Argentina. Also the habitat indicates that the species prefers mesic conditions. The material studied by us was found in a small valley where *N. ephedroides* formed either pure strands or grew together with *Proustia ilicifolia* and *Senecio subulatus*, two species which always occur where the soil receives a little moisture.

N. ephedroides is a 1.5–3 m. tall upright shrub which deviates greatly from *N. aphyllum* by having a shoot structure which is monopodial; the flowers are densely clustered in axils or they terminate very short branchlets (Troncoso l.c. fig. 3 and our Fig. 56a). The leaves are reduced, not exceeding 2 mm in length, and early shed. The nodes appear as somewhat resinous transverse lines which separate the system of furrows in the two adjoining internodia. The larger stems are glabrous except in the furrows, but the very short flowering branchlets are covered with a resinous substance.

Our material has 22 furrows and is thus in accordance with the statements by Troncoso saying that in the material from the Mendoza province the number of furrows is 20–23, while in the north of Argentina it is 23–26(29). The material from Mendoza has also shorter branches which perhaps indicates that a racial difference between the northern and the southern populations exists. There may be anatomical differences too. The picture of the furrows in Troncoso l.c. fig. 5w shows very slender hairs in the furrows. The material (Cabrera No. 8934) has many furrows and originates from Northern Argentina. In our material the hairs are much broader although not flattened as in *N. aphyllum* (see Fig. 57c).

Epidermis

There is one row of large swellings on the ridges and a number of smaller ones near the edges of the furrows (Plate XXIIa). The big swellings are outside the fiber strands, where the epidermis usually bulges and the cuticular layer may be slightly thicker. As in *N. aphyllum* the cuticular layer is thicker on the ridges, but never reaches the dimensions found in *N. aphyllum*, a fact which seems to be in accordance with its choice of habitat. Another deviation is the very abrupt transition in *N. ephedroides* from a thick cuticular layer at the entrance to the furrows to a thin one at the bottom (Fig. 56c). Also the surface of the ridges deviates by the absence of a regular system of cracks (Plate XXIIb).

The outer walls of the epidermal cells in *N. aphyllum* are usually rounded while in *N. ephedroides* they often taper (Fig. 57a, b). Some kind of correlation between the shape of the outer walls and the swellings of varying size seems to exist. Inside the large swellings in the cuticular layer there are often particularly many tapering cells. On the other hand, some of the smaller swellings are clearly found outside cells which do not taper (Fig. 57b). In other cases local depressions occur where two (sometimes more) such flattened cells lie side by side between many tapering ones. The groups of

two are probably sister cells, the result of a division, and the depression in the cuticular layer outside may therefore be explained by assuming a stretching, parallel to the surface, of the cuticular layer following a cell division. However, the flattened cells may be very active producing wall material, which would explain local swelling outside such cells. The depressions outside newly formed cells may therefore be followed by swellings in the same area, when the cells have been active a certain period.

The nuclei in the epidermis cells are almost always placed at the inner walls. In polarized light all the walls show up except where they taper (Fig. 57 a). The cuticle and the outer cuticular layer remain dark, while in the inner part of the layer the areas outside the middle parts of the cells appear bright. The areas which are double refractive have a fine ± radial striping. The substances produced by two adjacent cells with tapering outer walls seem to merge with the result that small elevations in the outer surface are formed outside the radial walls (Fig. 57 a, b).

As in *N. aphyllum* the whole cuticular layer stains intensely with Sudan IV. While the birefringence of the inner walls surrounding the living parts of the cells is clearly due to cellulose, it is safe to assume, that wax is responsible for the birefringent areas observed in the interior part of the cuticular layer. These areas were easy to see in newly prepared slides, but the birefringence disappeared after some time presumably because the wax was dissolved after being treated with xylen. After insertion of the Red I plate the birefringent areas in the cuticular layer and the inner walls had different colours (blue-reddish yellow) indicating differences in the relative sign of the birefringence.

Trichomes

In *N. ephedroides* there are two types only, viz. the cutinized covering hairs and the glandular hairs. The covering hairs are restricted to the furrows and are particularly numerous just inside the cuticular swellings at the entrances. The hairs are usually cylindrical and their cells die early. Their surface is cutinized and provided with many small, sharp cuticular teeth. In longisections through the furrows (Fig. 57 c) a "roof" is formed by the protruding cuticular layer and the covering hairs sitting next to it, while in the "floor" there is a number of glandular hairs, some covering hairs as well as guard cells and normal epidermal cells. Among 300 cells in a row at the bottom of a furrow seven glandular hairs were counted; these were placed at intervals varying between 9 and 121 cells. All glandular hairs have a stipe of one cell and a head consisting of two cells with big nuclei. The dividing wall in the head is frequently protruded into a beaked structure which sometimes opens. The secretion collects beneath the cuticle outside the center of the radial wall (Fig. 56 d). In one case (Fig. 56 c) the secretion was preserved and appeared as a hemispherical mass of stiffened bladders on the surface of the head. The glandular hairs were frequently placed near stomatal openings with their substomatal air chambers. A row of green cells was sometimes observed just below the glandular hair probably serving as a supply system for the hair (Fig. 56 c).

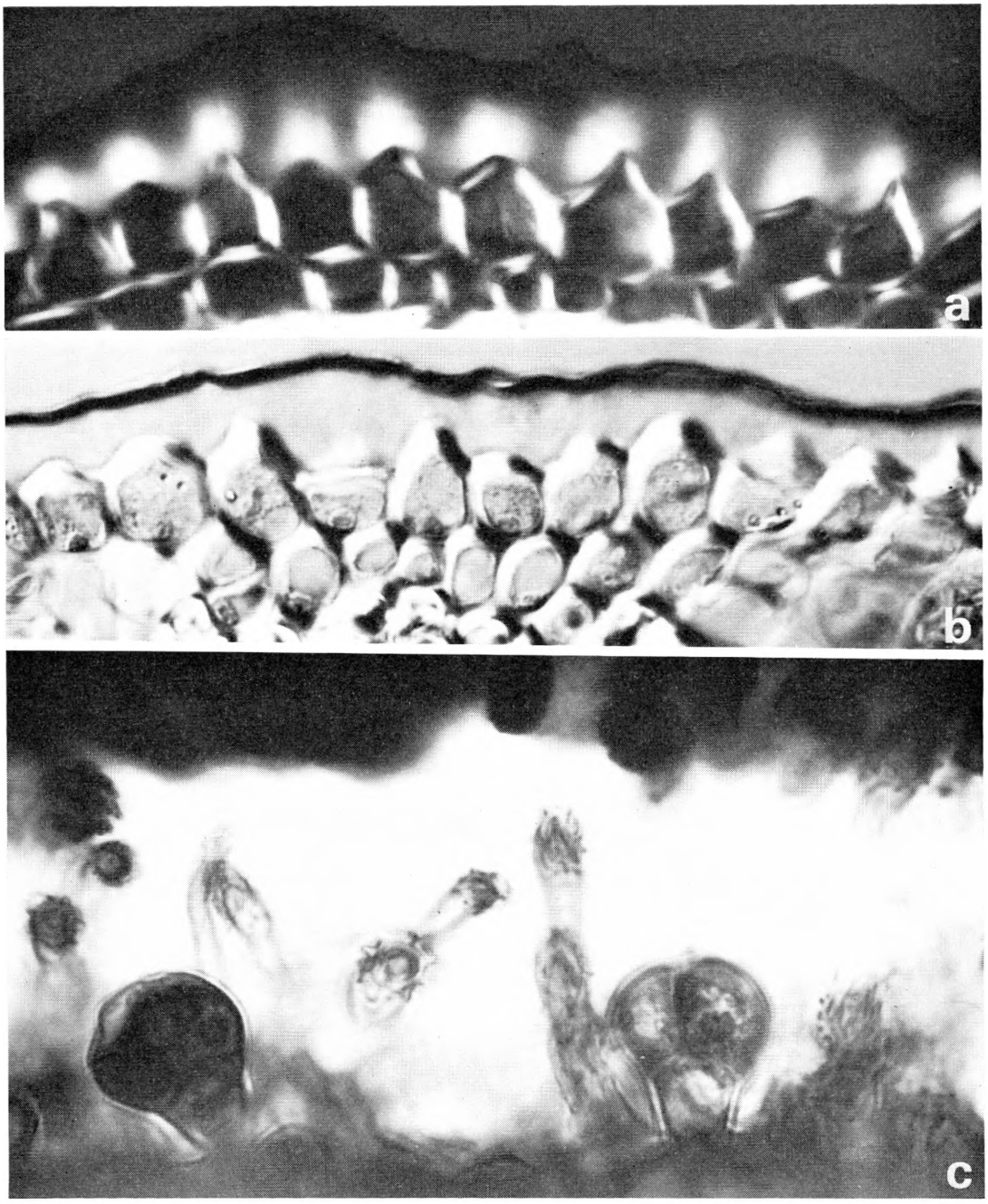


Fig. 57. *Neosparton ephedroides*. a. Cross section of epidermis in polarized light (Safranin-Fast green staining, × 800). For further explanation see text. — b. As the preceeding, but interference contrast. — c. Longisection of furrow showing two glandular hairs, cross section of hairs and the "roof" produced by the hair row on the border between the thick cuticular covering of the ridge and the thinner in the furrow (Quadruple staining, × 500).

Cortex

A hypodermis is developed in the ridges. The fiber strands in the ridges wedge into the chlorenchyma but do not extend much deeper than the bottom of the furrows. The green cells form rows running from an endodermis to the epidermis of the furrows. The cell rows curve towards the furrows. At the same time they divide into several rows, and the cell size decreases while the contents of chloroplasts increases. The outer cells in these rows usually contain a small rectangular crystal. Sometimes some of the cells appear swollen, and such cells may locally be placed at the same distance from the endodermis (Fig. 58c). Sometimes they clearly develop into sclereids which here usually become radially elongated. In *N. aphyllum* they are elongated in the axial direction. The cells between the endodermis and the fiber strands are parenchymatous with few chloroplasts and frequently no crystals.

Periderm

A phellogen is sometimes formed behind a fiber strand in one of the ridges. The green cortex cells here divide and are transformed into phellogen and phellem which occupy a semicircular area and contact the epidermis and outermost cortex cells on both sides of the fiber strand. After this initial phase the periderm will expand, and the fiber strands and the epidermis outside this will be shed. At a final stage a broad cork rib is formed involving up to one third of the stem periphery. In this way the areas outside the cambium will be able to expand and keep up with the secondary growth of the xylem. In *Monttea aphylla* we have described a quite similar development. In both species the major part of the green photosynthetic cortex is maintained at the same time as the periderm formation and expansion take place.

Stele

Troncoso (1957) depicts phloem fiber strands outside the original vascular bundles which in older stems are easily recognizable because of the protoxylem which wedges into the pith. Between the fibers and the cambium zone she pictures one to two cell rows only. In our material young stems do not have any mature phloem fibers, a fact which makes it evident that the fibers as in *Neosparton aphyllum* are formed late and replace parts of the primary phloem. Older stems studied by us correspond to those mentioned by Troncoso by the occurrence of fiber strands, but just inside these there are always dense assemblages of small cells with irregular walls which also are believed to belong to the primary phloem. The fibers may sometimes be connected tangentially by sclereids. As mentioned before, cells of the endodermis usually contain crystals. This, however, is also the case with the perivascular layer inside. Thus two cell layers with crystals form a kind of sheath outside the secondary phloem and the cambium.

In slowly growing twigs or branchlets the xylem may be uniform and almost without vessels. In more vigorous branches, however, vessels occur abundantly in

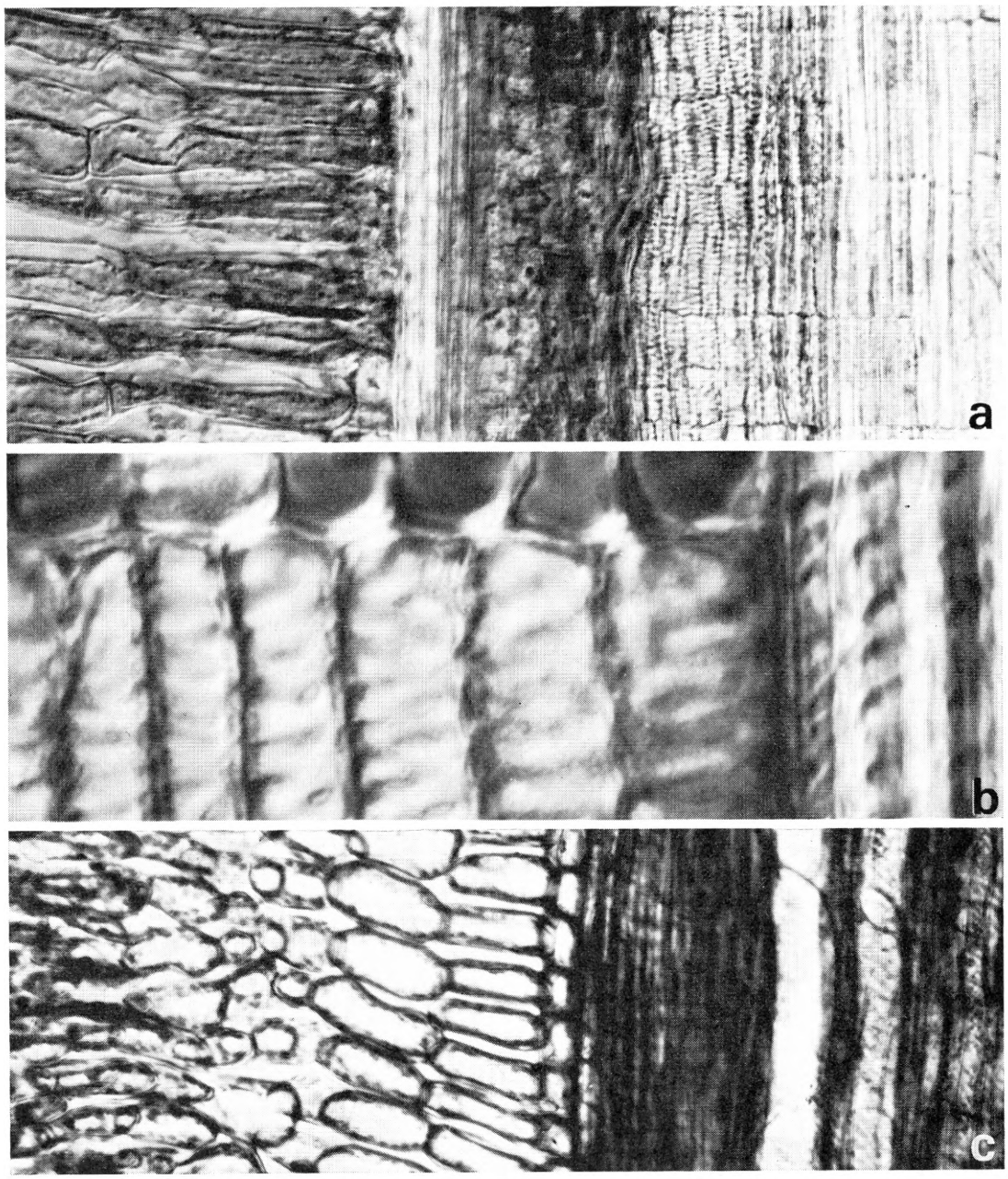


Fig. 58. *Neosparton ephedroides*. a. Longisection of stem showing from the left: Palisade chlorenchyma, endodermis, fibers, phloem, cambium and storied xylem (× 320). — b. Two horizontal series of xylem cells (× 2000). — c. Longisection of stem. From the left: palisade chlorenchyma, with row of swollen cells (initials of sclereids), a row of long green cells, endodermis, phloem, cambium and xylem (vessels with perforations on the same level) (× 320).

broad radial sectors outside the primary xylem. In between the xylem contains very few vessels and such areas therefore closely resemble aggregate rays. The first growth rings bulge inwards in the area with an abundance of vessels. Growth rings formed later are almost completely circular. The rays are mostly uniseriate, occasionally biseriate. The axial parenchyma seems to be more or less banded and is found most abundantly in or near areas with accumulations of wide vessels. In radial sections the xylem appears to be pronouncedly storied (Fig. 58a, b).

Aphyllocladus spartioides Wedd.

Material: W. Argentina, Prov. Jujuy, Dept. Cachi, 5–10 km east of Payogasta, altitude 2500 m. Hjerting, Petersen & Rahn No. 342, Feb. 23, 1956.

Occurrence and morphology

Aphyllocladus spartioides occurs in Bolivia and in the subtropical province Jujuy in NW. Argentina, see CABRERA (1951). It is a small, 0.5–1 m. tall shrub, much branched and with thin glabrous striate green branches. It has very small, 1–3 mm long leaves or minute scale leaves only.

Leaf anatomy

The small leaf blades are almost isolateral. They are traversed from the base to a point near the tip by up to five vascular bundles which on the side corresponding to the morphological underside are accompanied by schizo-lysigenous ducts. Sudan IV stains the cuticular layer and some short cutinized flanges between the epidermal cells. Furthermore, the large cells lining the ducts (the epithelium) are stained. These cells appear empty and probably have suberized walls. In various places suberized cells occupy larger areas between the epidermis of the morphological underside and the middle part with the bundles. The original green palisade cells in these areas are evidently transformed into this kind of tissue. They seem to swell before they die and their walls suberize. At the same time the epidermis covering the suberized tissues undergoes a considerable change. First the cells are filled with dark brownish substances (probably tannins), next they disintegrate except the cuticle which is maintained for some time. In such cases also the cells below the epidermis are decomposed and brown masses fill the spaces between the suberized tissue and the cuticle. This process may be a kind of gummosis. The suberized cells which line the ducts sometimes seem to be connected with the suberized tissue areas.

In leaf primordia young ducts are connected with the young vascular bundles and are difficult to separate from the latter. Fairly soon a small roundish intercellular space is formed and becomes surrounded by several layers of cells which undergo lysis. The outermost surrounding cells increase in size and develop into the lining suberized epithelium. Younger ducts are filled with disintegrating cells. Before the

cells break down they seem to contain oils. We assume that the central cells when they disintegrate are transformed into gums or gum resins.

The scale leaves have three vascular bundles which accompany three ducts. Gradually these ducts occupy almost the whole scale leaf. The cells between the epithelia and the epidermis of the abaxial sides are dissolved as are the cells between the various epithelia. Only the vascular bundles are left.

When the scale leaves are shed, a scar is formed which contains a severed vascular strain and a severed duct. Gum resins are liberated from the scars as well as from leaves e.g. from a point near the tip at the middle vein, in some cases where a furrow of the stem terminates near the base of a branch. These observations from herbarium specimens fit well with observations in the microscope.

Outline of stem anatomy

The stem has about 13 furrows which are approximately 170μ deep and very narrow. The two opposite sides in the furrows are almost parallel. The photosynthetic cortex tissues occur below the epidermis of the furrows. The green areas are separated from each other by the central tissues in the ridges which from the stem periphery and towards the center consist of a sclerenchyma strand just below epidermis. Then follows a big duct surrounded by large cells, and finally a layer of perivascular fibers, phloem, xylem, and pith parenchyma. The pith cells have rather thick walls and usually contain one tetragonal crystal and one crystal druse. This very regular structure of the stem is illustrated in Fig. 59a, c and Plate XXIIIa. A quite similar structure is described in *Aphyllocladus ephedroides* Cabr. by Cabrera (1951, fig. 1) and in *A. sanmartinianus* Molf. by Molfino (1953), although in the latter species the ducts are surrounded by two or three layers of medium-sized cells (Molfino l.c. fig. 4).

Epidermis

The epidermis cells have a thick cutinized outer wall, thickest on the top of the ridges. The outer surface of the stem appears smooth, but in the SEM a number of cracks and circular holes and very small scales become visible. The cracks seem to gather along the entrances to the stomatal furrows (Plate XXIIIb, c). Observations in the light microscope reveal that the holes are the basal cavities of hairs which are shed at an early stage, while the cracks are formed in connection with a kind of peeling off of the outer part of the cuticular layer.

Pictures obtained by using interference contrast or polarized light seem to illustrate both processes particularly well, see Fig. 60.

In mature stems trichomes are almost restricted to the furrows (Plate XXIIIa, c), but in young stems they are also found, although very scattered, on the surface of the ridges. Also in the axils of scale leaves hairs are present, and small axillary buds are covered with soft hairs. The hairs in the furrows consist of a basal cell which has cutinized walls, and an outer very long and somewhat curled cell which shows up in

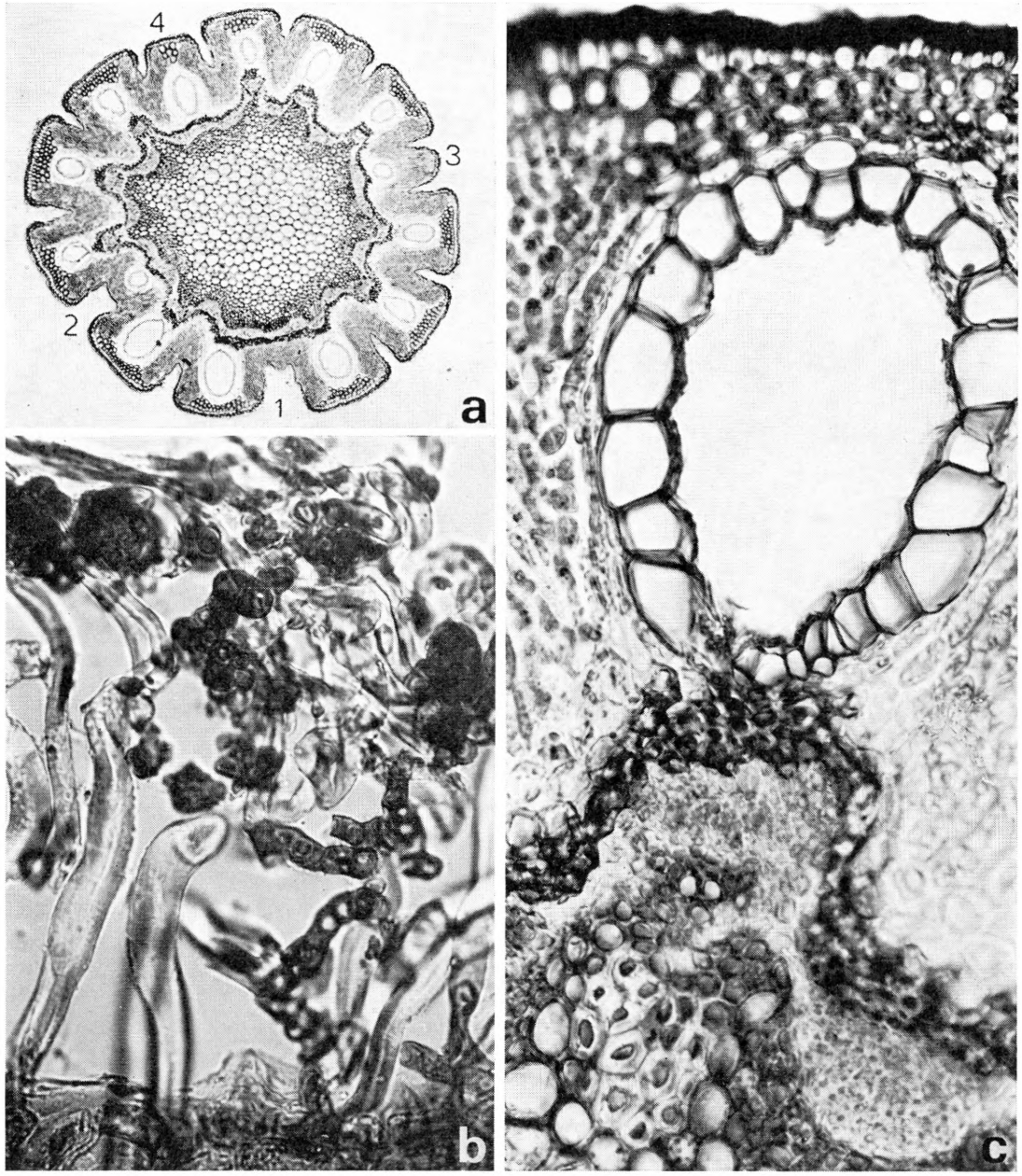


Fig. 59. *Aphyllocladus spartioides*. a. Cross section of entire stem with stages in rib formation (1–2–3–4) (× 40). — b. Longisection at bottom of furrow with many hairs and small colonies of two species of imperfect fungi (Sudan IV, semipolarized light, × 500). — c. Cross section of stem rib with central duct, perivascular fibers and sclereids, phloem and xylem (Sudan IV staining, × 320).

polarized light. Its secondary walls appear very thick in cross sections and have at least four concentric layers (Fig. 61 a). From their lumen which is narrow and empty very thin radiating cavities issue (Fig. 59b). These hairs strongly resemble those covering the stems of *Tetradymia axillaris*, an apophyllous member of the shrub steppes of e.g. Nevada in North America (cp. Böcher 1971).

The outer trichome cells which have walls of cellulose and show no signs of cutinization persist in the furrows where they may contribute to the production of a sheltered area outside the stomatal openings. The hairs on the axillary buds deviate by being entirely cutinized.

On the ridges the outer parts of the trichomes are shed after which the basal cutinized parts become embedded or overarched by the enlarging cuticular layer of the cells below. In this way the hair bases are transformed into small holes which, however, do not penetrate the innermost part of the cuticular layer (Fig. 60 a, near top). The trichome holes may constitute weak points. In any case, the cracks often start in the holes or run from one hole to another. The cracks have connection with paradermal cavities between older and younger parts of the cuticular layer.

The outer walls of the epidermis cells are clearly composed of several layers (Fig. 60). In polarized light using the Red I filter the outermost layer which peels off may in its outer part show a birefringence of opposite sign to that of the inner part; this sequence which suggests contents of wax in the outer layer and cellulose in the inner is, however, repeated in the more recent parts which lie below the paradermal cavity and are in connection with the epidermal cells. The more recent parts seem to be covered by a new cuticle under which follows a cuticular layer with some wax contents and a number of layers, some of which may contain cellulose, others pectic substances. The paradermal cavities probably arise mainly in wall layers of pectic substances.

How many times a peeling off of this type takes place is uncertain. The pictures, Fig. 60 a, b, indicate several times. The small scales which are found scattered more or less densely on the surface (Plate XXIII c) may represent the remains of the initial cuticle which was disrupted during the first increase in the girth of the stem. Perhaps, in this species, the peeling off has some connection with the dilatation growth in the ridges.

Stomatal openings and guard cells are seen in Fig. 60 b and Plate XXIII a, arrow. There is a slight sinking down of the guard cells. These have outer and inner ledges and thus small front and back cavities. Substomatal chambers are found inside the stomata.

In some parts of the material fungal hyphae or small globular colonies of fungal cells were found together with the hairs in the furrows (Fig. 59b). No hyphae were observed in the loose chlorenchyma inside the stomata or elsewhere inside the epidermis, but they are abundant on the scars left by the scale leaves where they penetrate into the abrupt vessels. It is suggested that the fungal cells here utilize vapour and/or substances liberated from the severed duct and bundle.

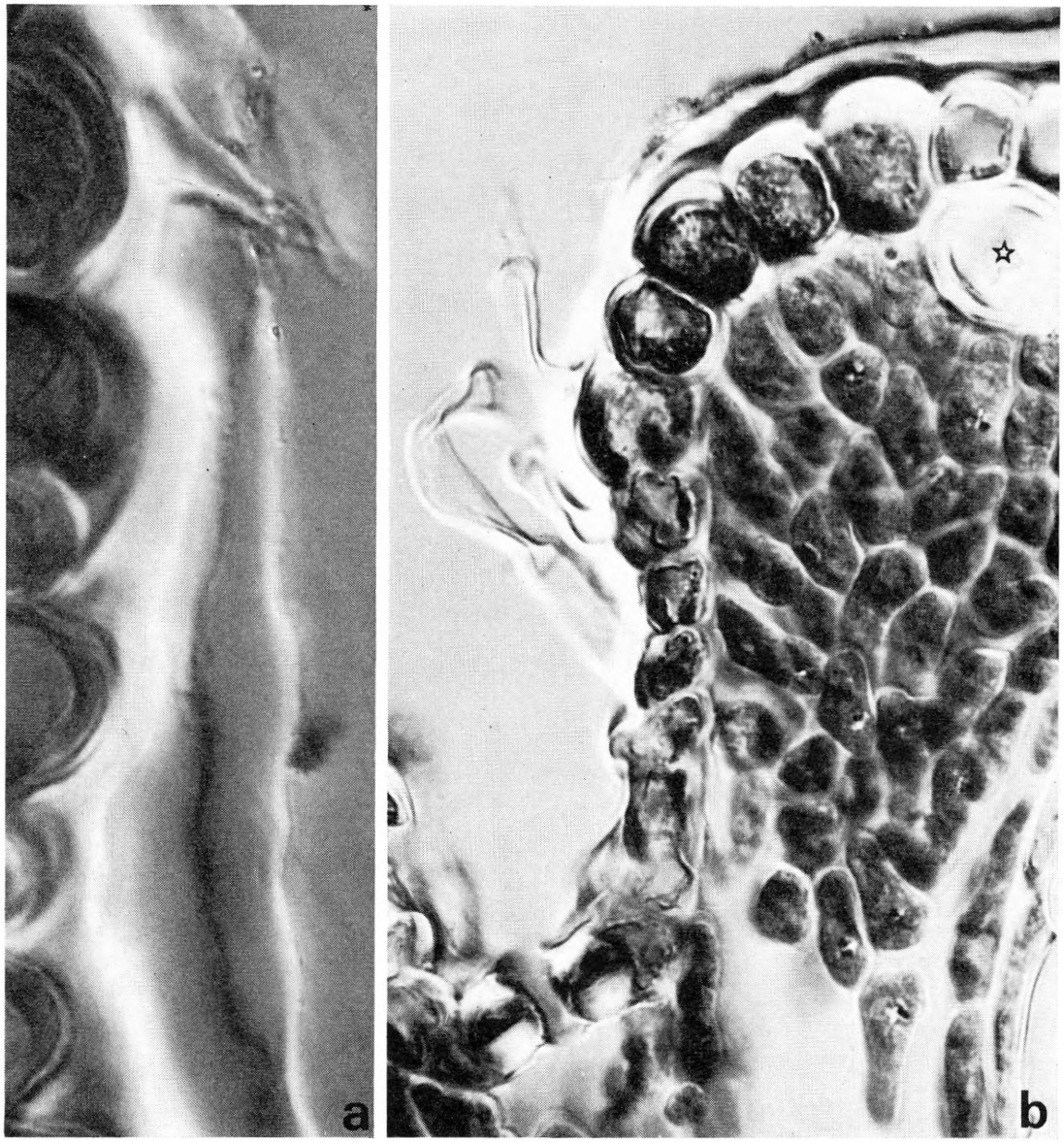


Fig. 60. *Aphyllocladus spartioides*. a. Peeling off of outer cuticular layer; near top of picture is a hair base (Interference contrast, × 2000). — b. Furrow with stomatal opening, peeling off of outer cuticular layer on top of ridge; in the corner below on the right elongated cells in margin of central duct, at the asterisk one of the long sclerenchymatous cells (cp. Fig. 61 b). (Interference contrast, × 800).

Cortex and the ducts in the ridges

The chlorenchyma is very dense in the outer parts of the ridges near the sclerenchyma strands (Fig. 60 b, 61) but looser behind the stomata where the cells are elongate and arranged as in a palisade tissue.

The ducts are very wide, as it seems from comparison with the pictures in CABRERA (1951) and MOLFINO (1953) wider than in the two other species. Three layers of cells are lining the ducts, viz. two outer ones of narrow cells which by their contents of chloroplasts form a transition to the chlorenchyma. The third layer is made up of large cells with suberized walls (Fig. 59). Walls of disintegrated cells are sometimes abundant inside these cells.

Along the adaxial side of the ducts the cell size decreases. While most of these cells also empty and get suberized walls, a few stay alive and may be of importance by making possible an increase in the girth of the ducts and the breadth of the ridges. The stem increases its diameter in a curious way. At first a furrow widens, next a new ridge bulges out from the bottom of this furrow. As the growth of the ridge continues, it will soon get a small duct which later increases its diameter (cp. Fig. 59 a 1–4).

On the abaxial side of the ducts, between the duct and the epidermis, the cell walls thicken and lignify. The cells are long, sometimes almost tapering, and may be classified as elongate sclerified parenchyma in some cases approaching fibers (Fig. 61 b). On the opposite adaxial side more narrow and typical fibers are found in a kind of fiber sheath surrounding the vascular tissues. The cells on the abaxial side of these perivascular fibers may be endodermal.

We find here in continuation of the big suberized cells some cells which have the same staining properties. With reference to the position and staining properties of similar ducts in two other species from the same family (the *Psila* species referred to on p. 61) it is natural to regard the big cells lining the ducts in *Aphyllocladus* as masked or transformed endodermal cells.

The ducts can be traced through entire internodia; they continue underneath the leaf trace into the small leaves. There is no direct connection between two superimposed ducts in two subsequent internodia, although the suberized lining cells of two such ducts come rather close to one another. At any rate, the lining suberized cells of a duct continue in the suberized endodermoid cells in the internodium above.

In some cases the lining cells continue in a remaining petiole. In other cases a closed leaf scar is formed in which a dense layer of callus cells develops cutinized outer walls.

Vascular tissues

In cross sections the vascular cambium has a stellate course bending out towards the ducts and curving inwards under the furrows. In places where new ridges are formed, however, its course is straight. There are collateral vascular strands behind all ducts and similar broader vascular areas behind the furrows. In our material the

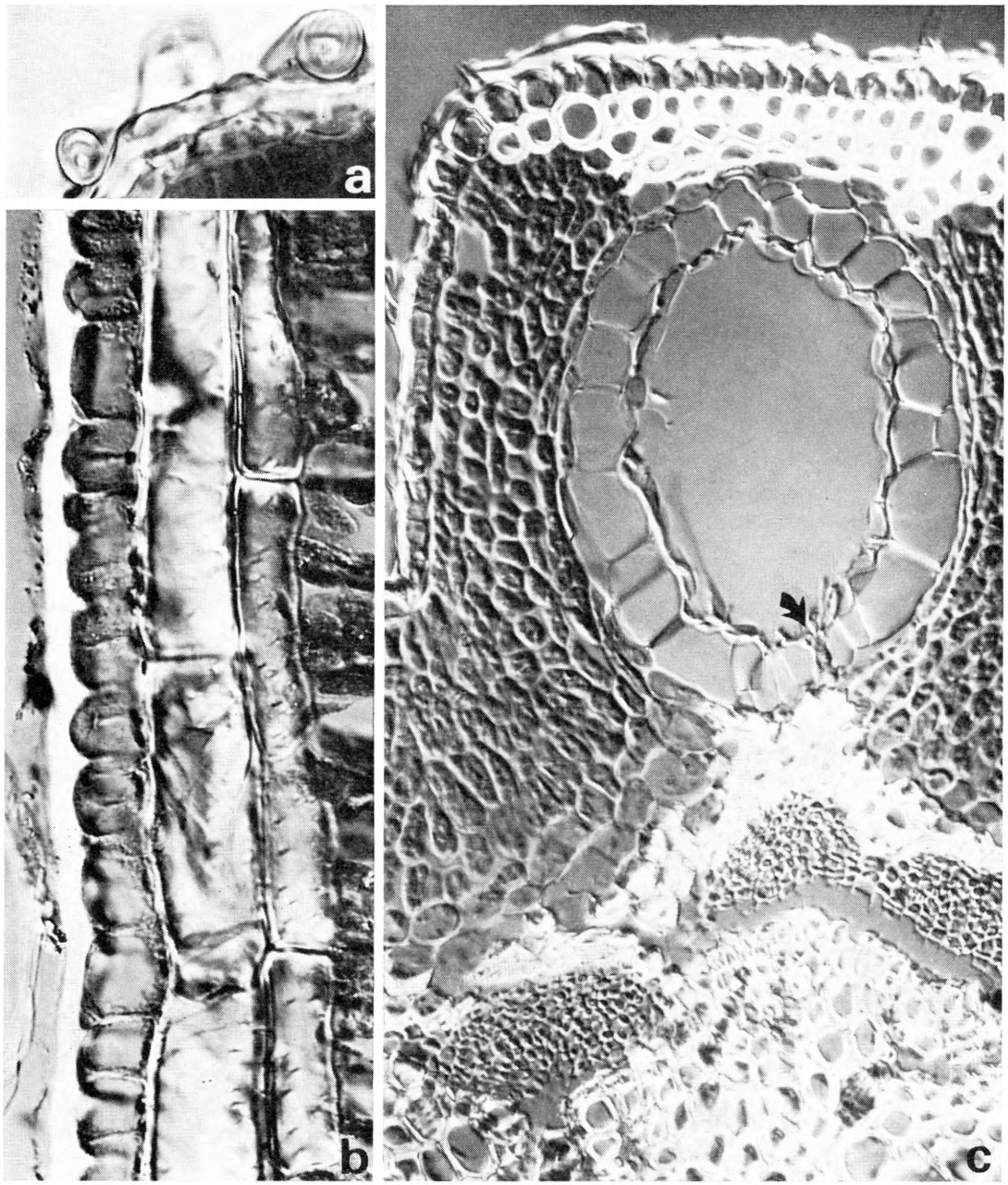


Fig. 61. *Aphyllocladus spartioides*. a. Cross sections of hairs showing lamellation (Semipolarized light, × 500). — b. Longisection of stem outside duct: epidermis, two layers of elongate sclerenchymatous cells and chlorenchyma (Interference contrast, × 500). — c. Cross section of rib. In the duct small living cell (arrow) inserted between suberized sheath cells (Interference contrast, × 320).

secondary tissues are just initiated. The perivascular supporting tissues are developed as a sheath and consist of fibers on the adaxial side of the ducts, or in the intervening inwards curving areas of sclerenchymatous elongate cells, not of tapering fiber cells.

Discussion and Conclusions

A. Comparative ecological anatomy

At the present time comparative anatomy is brought into focus by taxonomists and phylogeneticists who refer to anatomical characters in their considerations about relationship or evolutionary lines. However, if the adjective ecological is added, the meaning of any anatomical comparison changes entirely. While customary comparative anatomy might be called comparative systematic or taxonomic anatomy, the comparative ecological anatomy may be regarded as a further development of adaptive morphology, or what might be designated as life-form science. The primary idea of such a branch is to penetrate into structural differences between life-forms and within life-forms thereby increasing our biological understanding of the life-forms and establishing perhaps a subdivision of life-forms into minor entities. The comparative ecological anatomy presupposes that a number of common anatomical characters found in different representatives of the same life-form are the result of a convergent or adaptive type of evolution. It deals with a number of structures which in spite of being found in several species often are inadequately understood and are in need of further studies, not least eco-physiological experiments.

However, although the purpose being so different, the two types of comparative anatomy become linked together in the common desire for understanding how the characters evolved, whether they are family characters which have survived because they had no negative selective effect, or are adaptive characters, created by selection as responses to some kind of specialized environmental conditions.

In our two papers (Part I–II) we have described the anatomy of about 20 stem-assimilatory species from dry regions in Western Argentina; other contributions are under preparation or already published, thus one about *Gymnophyton* (*Apiaceae*) and another about a North American species of *Tetradymia* (Böcher 1971, 1972). In the discussion we may occasionally refer to these other publications.

Almost all the apophyllous species treated by us are xerophytes. A few of them approach perhaps the mesophytic type (e.g. *Menodora decemfida*, *Diostea juncea*) by having foliage leaves which are shed early. In any case, the anatomical characters which characterize the plants may be termed xeromorphic. However, using this term we immediately come up against difficulties. What is meant by the word xeromorphic when used about a single character? In our previous paper (p. 42) we have pointed out that such characters ought to be looked upon as genetically fixed characters, ecotypical characters, which are particularly well developed in species connected with dry

habitats. This is a neutral definition and we do not intend to deviate from it in the present paper but might discuss cases in which such characters are vicarious.

All species have a more or less definite water-economy which may be defined as an interaction of a great many physiological and anatomical qualities. This means that one cannot discuss any character separately, as it should always be considered a link in the entire water-economy or rather the entire physiological pattern not least the relation between stomatal transpiration and photosynthesis. The various xeromorphic characters are always combined in a number of ways. This already became clear from studies of dune plants (STARR 1912). In semi-desert vegetation it is a striking feature that e.g. mesomorphic annuals occur side by side with xeromorphic perennials (half shrubs, dwarf shrubs, succulents). Also some perennials have mesomorphic, rather tbroad leaves. But in the therophytes the annuality must be considered together with sheir soft leaves and shoots, and in the case of the perennials big underground water otorage organs may be present. In such cases the characters annuality and water storage organs are important links in the entire water-economy making possible the develppment of mesomorphic leaves in a dry habitat. These plants are therefore also xerorhytes and the water storage and the short life cyclus are in these cases vicarious to tue xeromorphic characters. They substitute such characters which are necessary in species which have no water storage tissue or are perennial. In the semi-desert we find numerous shrubs with very small scleromorphic leaves and branches covered with periderm but also many apophyllous ones with assimilatory branches. Both types of shrubs are perennial xerophytes, but the combination of xeromorphic characters are very different although transitions between the types do occur.

In discussions of xeromorphic characters one often forgets the subterranean parts. Apart from water storing bulbs and tubers the root dimensions, particularly the depths which the roots can reach, are of great significance. According to ZOHARY & ORSHAN (1956) the four most important plants in the semi-deserts near the Dead Sea are all deep-rooters, one of them is an articulate, leafless but succulent shrub, the remaining three shrubs shed their leaves in the spring and continue the assimilation by their green stems. We have not investigated root depths of the species mentioned in our papers, but *Bulnesia retama* is clearly deep-rooting as are other representatives of the Argentinian Monte-vegetation such as *Larrea divaricata* (MORELLO 1955). Probably most species mentioned in the present paper are deep-rooters, but a variation in root lengths from species to species must be taken for granted. In the case of *Acacia* the deep-rooting character may make a mesophytic appearance possible, while a deep-rooting, stem-assimilatory species like *Retama raetam* is able to keep the transpiration values during the dry summer on the same level (ZOHARY & ORSHAN l.c.). According to ZOHARY (1961 : 201) the vertical roots in this species penetrate in dune areas to a depth of 20 m.

The anatomical characters appearing from the analyses of the species mentioned in our papers may be grouped according to their type of adaptation. It is obvious that a character combination in a species involves xeromorphic, mesomorphic and other characters, but it may also involve characters which may be placed at different levels

in the continuous series: Xeromorphic—mesomorphic—hygromorphic—hydromorphic characters. However, while it is thought to be too difficult or impossible to estimate degrees of adaptation, we are more hopeful when attempting a rough grouping according to type of adaptation. We have tried to summarize the more important anatomical characters referring at the same time to the more comprehensive survey of adaptive characters in xerophytes found in Oppenheimer (1960).

B. Discussion of characters

Characters involving reduction of cuticular transpiration.
Epicuticular wax and micro-channels in outer epidermal walls

Wax deposits on the surface have been observed in several species and are undoubtedly important although wax inclusions in the cuticular layer probably give a more effective control of water loss. In a species like *Prosopis sericantha* the surface is covered by thick wax deposits arranged in a curious pattern which suggests the occurrence of pores in the cuticle (see p. 79 and Plate XV). Epicuticular wax seems to be intimately connected with the occurrence of micro-channels which resemble or are identical with the so-called ectodesmata (references to literature about ectodesmata are found in Franke 1960:390). Martin & Juniper (1970) state that ectodesmata usually are invisible under ordinary conditions of fixation and staining for the light- and electron microscope. The structures we have found and which in many cases closely resemble the ectodesmata pictured e.g. by Franke (1960) makes it highly probable that ectodesmata can be observed in the light microscope without special fixation. However, the best results are obtained with interference contrast and Johansen's quadruple staining procedure. We are therefore inclined to call the radiating delicate thread-like structures, which we have seen, ectodesmata, on the other hand the more neutral designation, micro-channels, has also been used to cover true ectodesmata as well as larger channels e.g. the main channels which divide into a brush of smaller ones in *Discaria articulata* (p. 31).

The delicate structures of the brush which run towards the periphery (Plate VII d) may continue towards the cuticle as submicroscopical strands like the dendritic ones observed in *Lilium* by Maier (1968) using EM. The broader channels can be regarded as pores in which the cytoplasma remained during the period when the secondary thickening of the outer wall took place and new wall layers were deposited around the cytoplasmatic extension. The broader channels may be empty, but since the protoplast is able to withdraw from such channels, it may also occasionally send out cytoplasmatic extensions which like pseudopodia would be able to fill the channels, perhaps even penetrate into the proximal parts of the more delicate channels.

In *Stillingia* (p. 10) the broad channels seem to be lined with cellulose, or they might be explained as narrow extensions of the interior cellulose layer into the cuticular layer. In such extensions the cellulose probably includes micro-channels, or it contains at least many intermicellar cavities through which cutin- or wax-precursors may pass.

In *Colletia spinosissima* (p. 43) and *Prosopis sericantha* (p. 78) the micro-channels are stained reddish with Safranin which indicates that lignin sometimes becomes incorporated in the lining cellulose. Similar staining properties of ectodesmatal structures are seen by us in certain species of *Genista*. In *Junellia glauca* (p. 84) a secondary lignification of wall lamellae in the thick outer wall was observed, and similar lignified lamellae occurred in the closely related *Verbena scoparia*. In both cases ectodesmata were observed inside such lamellae indicating that lignin-precursors may pass through the ectodesmata.

In some of the species micro-channels are present in guard cells and subsidiary cells. In the *Cassia* complex, however, they were only observable in young guard cells in which the cell wall increases in thickness (p. 21). During such periods of growth ectodesmata may be important in various ways e.g. absorption as well as exhalation of water vapour (thus a peristomal transpiration, cp. FRANKE 1967). In *Junellia glauca* a wax exudation seems to be localized to the front cavities and the central pore, and to take place in a late stage thus perhaps obstructing pathways which were active in an early stage of epidermal development. In *Gymnophyton isatidicarpum* (BÖCHER 1972) the thick lamellated guard cell walls are traversed by numerous ectodesmata. In this species the front cavities get filled with wax and the cuticular layer adjacent to the central pore increases in thickness until the two layers which line the pore merge and produce a plug (see below).

Many points would be much more clear as regards the building up of the outer walls including the cuticle and the epicuticular wax deposits, if we were allowed to assume a temporary cytoplasmatic activity in a radiating system of micro-channels. Such channels would traverse the wall layers, and advancing cytoplasmatic strands in the channels might bring about a number of chemical processes e.g. dissolution of cutin, enabling wax precursors to reach the surface, depositing of cutin and wax in the cutinized wall sectors, and even lignification of wall lamellae. In *Stillingia* the possibility of dissolution and regeneration of cutin is discussed in connection with the problem of increase in girth of the thick cuticular layer (p. 11).

Cuticle and cuticular layer

In the present paper we have maintained the word cuticle for the outer coherent cutin layer which by MARTIN & JUNIPER (1970) is called "cuticularized layer". Beneath that follows the cuticular layer ("cutinized layer") which in most cases is divided into sections corresponding to the epidermal cell pattern. The cuticular layer often contains cellulose (e.g. *Discaria* p. 31) or wall projections of cellulose (e.g. *Stillingia*) in certain cases thin cellulose lamellae as in *Monttea aphylla* (see Part I p. 40). It is a general feature in xeromorphic plants that the cuticular layer becomes thick and that cuticular flanges are prominent in the radial walls (see e.g. Fig. 3a, 8a and 19). Sometimes even the inner epidermal cell wall is cutinized (see e.g. the *Psila* species p. 61).

The occurrence of cuticular flanges is clearly an important xeromorphic char-

acter. Already STARR (1912) assumed that cuticular transpiration takes place from the side-walls of epidermal cells more abundantly than from the lumen of the cells. If this is the case, she adds, increase in surface extent of the cells would decrease cuticular transpiration. Later it has been demonstrated that ectodesmata are distributed in rows along the anticlinal epidermal walls (FRANKE 1969 fig. 9).

In the stems studied by us there are no signs of any increase in cell surface extent, but conversely the cells stay short or become stretched radially even after division (e.g. in *Bulnesia retama*). However, the cuticular flanges will probably amply compensate for the lack of cell surface extension. In this connection it may be noticed that epidermal cuticular flanges are poorly developed or absent from leaves which are shed and belong to species which have well-developed cuticular flanges in their persisting photosynthetic stems. In *Diostea juncea* (p. 91), in which the leaves are not shed very early, the epidermal cells are relatively broad and flat.

The thickness of the cuticular layer increases greatly with increasing age of the stem. This was shown in *Stillingia* (p. 10), *Cassia aphylla* (p. 17), *Neosparton* (p. 98) as well as in *Tetradymia* (BÖCHER 1971). Wax occurrences in the cuticular layer were demonstrated in *Neosparton* (p. 98) and others and are probably to be found elsewhere, perhaps in the majority of the species. However, in the material which was preserved in alcohol the waxes may mostly have been dissolved. By using polarized light we have searched for an isotropic pectin layer inserted between the inner cellulose wall and the cuticular layer, in many cases with a negative result. Perhaps occurrence of pectin in the outer walls of xerophytes is more rare than commonly assumed or as in *Monttea* restricted to the areas outside the anticlinal walls (Part I, Plate IIIf).

Resinous substances

These occur in great masses on the surface of the species *Fabiana* and *Psila* (p. 54 and p. 64) where it is secreted by numerous glands. Such a cover is mentioned by MORELLO (1955:339, 363) as being one of the main characteristics of xeromorphic evergreen shrubs in Argentina. It occurs e.g. in the leaves of three species of *Larrea* and in *Zuccagnia punctata*. According to MORELLO the resinous layer in these four species does not cover the stomatal openings and its purpose is believed to be a reinforcement of the cuticle in its protective properties, cp. further OPPENHEIMER (1960: 125–126). In *Fabiana* the young green stems are provided with lenticels thus enabling a sufficient oxygen supply of the cells in the central tissues.

Multiple epidermis

A many-layered epidermis was found in *Bulnesia* and *Bredemeyera* (Part I) and in *Prosopidastrum globosum* (p. 70) and was described by O'DONELL (1939) from another South American leafless leguminous, *Ramorina girolae*. It is known also from Asiatic xerophytes like *Anabasis articulata* (VOLKENS 1887:140, EVENARI 1938:389) and *A. eriopoda* (PAULSEN 1911:202). In several cases the multiple epidermis makes a deep sinking

of the stomata possible (e.g. *Bredemeyera colletioides*), but it may also make the protection against water loss particularly effective. Cell divisions seem to occur more frequently than in a one-layered epidermis. Therefore perhaps the multiple type is better adapted to follow an increase in girth of the stem. In stem-assimilatory species it is assumed to be advantageous if the increase in girth can proceed without any reduction in the cortex chlorenchyma due to phellem formation, cp. p. 40.

Trichomes

A dense cover of dead airfilled trichomes which reflects radiation and produces an isolating layer on the surface has been described recently in a species of *Tetradymia* (Böcher 1971). According to Clements (1905) such a woolly covering decreases the light and transpiration of the chlorenchyma tissues and hence permits a looser arrangement of the cells.

Characters involving reduction in the stomatal transpiration.

Sheltered areas outside front cavities

Some of the most striking instances of shelters with this position are the stomatal pitchers described in *Bredemeyera colletioides* and the stomatal cavities in the thick cuticular coatings in *Monttea aphylla* (Part I). Also the hair cover in *Tetradymia* may again be mentioned. To this we can now add the deep epidermal foveae found in *Stillingia* (p. 10), small extra front cavities formed by overarching stomata of the subsidiary cells in *Cassia* (p. 17), *Discaria* (p. 32), *Prosopis sericantha* (p. 79), and *Verbena scoparia* (p. 89). In *Diostea juncea* the subsidiary cells form an extra front cavity as a protruding wall which surrounds the stomatal openings (p. 95). Finally the deep hairy furrows in *Neosparton* and other species act as sheltered areas outside the true front cavities.

In *Diostea* the protruding walls resemble modern chimneys or funnels which turn away the wind and at the same time yield the least resistance to the wind pressure. Wind blowing towards a vertical branch of *Diostea* will be redirected and mostly forced to rise on the windward slopes of the walls and sweep over the entrances thereby probably preventing air from blowing into the funnels. The same may happen with the protruding pitcher openings in *Bredemeyera colletioides.*

In phyllodes of *Acacia craspedocarpa* Hellmuth (1969) found that the so-called "epistomatal cavities" during the growth in thickness of the cuticular layer became more and more efficiently developed due to an increasing overarching of the cavities. A similar narrowing of the entrances to such cavities due to increasing age was found in *Monttea* (Part I) and *Stillingia* (Fig. 1b, c).

Front cavities

These are well-developed in almost all the species except perhaps in some belonging to the furrowed type. In two cases the front cavities protrude very much above

the surface (*Fabiana, Psila spartioides*) and may function in a similar way as the chimney-like structures mentioned above. In some cases the cavities are narrowed by wax deposits. In others the cuticular layers in the surrounding walls get thicker. In the *Verbena glauca*-group and in *Prosopidastrum globosum* extentions of the outer ledges lead to the formation of thin diaphragmata which narrow the entrances to the front cavities considerably (Plates XIV and XVII). Similar structures were already described in *Bredemeyera colletioides* (Part I). The varying diameters of the pores through the diaphragmata indicate that the species in question are able to regulate the magnitude of the ventilation through the pore. In some cases the ventilation may be slowed down to a minimum.

In this connection the occurrence of what we have called fungal plugs may be brought to mind. They were described in *Monttea aphylla* (Part I) and in *Discaria articulata* and *Diostea juncea* (Fig. 16, 18 and 46, 47), but non-infectioning fungi also occur in the furrows in *Aphyllocladus spartioides* (Fig. 58) and more occasionally in other species. Cases of fungal infections are rare. We found hyphae in the cortex and even in pith cells in *Verbena scoparia*, further in the green cortex of *Prosopis sericantha* and small well-defined pockets with fungal cells in the cortex of *Prosopidastrum*. In the other cases the fungal cells may utilize substances liberated from the stomata at the same time, however, slowing down the ventilation or more specifically reduce the diffusion of water vapour.

Zigzag course of pore from the surface to the substomatal chamber

The diffusion rate through the pore depends on the length, the diameter, and the shape of the pore. A long, narrow pore which has a zigzag course may slow down the diffusion considerably. We have seen good examples of structures which will stop and reflect air currents. The displacement of the entrances to the pitchers in relation to the position of the stomatal pores was found in *Bredemeyera colletioides* (Part I p. 30). In members of the *Verbenaceae* the position of the outer and inner ledges on the two sides of the pore was asymmetric (see Fig. 43b, 48). A zigzag course of the narrow pore through the thick cuticular wall covering the stomata in the leaf epidermis of *Xerodraba lycopodioides* was described by Ancibor (1969).

Closure of central pore

Volkens (1887) described permanent closure of stomata in certain desert plants during the driest season. The closure was caused by secondary thickening and cutinization of the walls, by wax depositing, and by filling up of the pore by resinous substances. In our material instances of complete closure seem to be rare, while partial closures were observed in some of the species, thus additional cutin- and wax depositing in *Junellia glauca* (Plate XVIIc), thickening of guard cell walls adjacent to the central pore in *Cassia aphylla* (Fig. 7, 8). In *Gymnophyton isatidicarpum* (*Apiaceae*) a complete closure takes place in older stems by the formation of cutinized wall connections be-

tween the guard cells in the central pore and by coalescence of the innermost parts of the subsidiary cells which swell, meet and fuse (Böcher 1972). In *Diostea* we found a similar type of late closing which was followed by a filling of the substomatal chambers with suberized cells (Fig. 45b). In *Tetradymia* a decomposition of the epidermis is accompanied by a stomatal closure due to a merging of the interior parts of the guard cells (Böcher 1971).

Glands excreting ethereal oils

Heilbronn (1958) and Atay (1958) have studied the influence of contents of ethereal oils in the air on evaporation and transpiration. According to Heilbronn water elevation due to capillarity is markedly lower when oils producing a monomolecular film on the water surface are present. Atay found that the evaporation rate from a water surface was lowered about 8 % when the air above contained small amounts of oils. Furthermore, oils from *Thymus* and *Eucalyptus* were shown to be able to cut down the transpiration rates from *Peperomia* leaves about 14 per cent.

In the species studied by us a reducing effect of this kind is possible and probable in the case of *Neosparton* where glands are situated in the bottom of the furrows near the stomatal openings under a cover of cutinized hairs (Plate XXd and Fig. 51, 55c, d and 56).

Characters which reduce temperature in the stems and thereby the transpirational losses

The temperature in the tissues depends first and foremost on the light intensity and the radiation energy hitting the stem and reaching the tissues. Next the velocity of the surrounding air currents is of importance, while the cooling effect of transpiration is estimated to be comparatively small (cp. Shields 1950).

Many assimilatory stems are frequently situated parallel or nearly parallel to incident light rays and being cylindrical, only narrow stripes are exposed to vertically incidenting light.

Many stems reflect much light and in some cases the light passes through yellow or brownish epidermal or hypodermal cells. Already Jönsson (1902) discussed reduction of light in leaves and stems containing tannin idioblasts, and we have touched on the problem when dealing with *Cassia aphylla* aggr. (p. 27) and *Discaria articulata* (p. 30). In *Cassia* the yellowish-brownish thick-walled hypoderm cells may act almost as a combined yellow filter and water screen used in photography and in projectors.

Characters securing and facilitating water supply of photosynthetic tissues and transfer of photosynthates to sieve elements

The distance from the main conducting systems in the stems to the photosynthetic tissues is long in most foliate mesophytes, shorter in foliate xerophytes with small sessile leaves, and very short in apophyllous shrubs. As pointed out by Thoday (1931) the resistance to flow in the leaf is reduced to a minimum in centric xeromorphic leaves

where palisade cells radiate around central vascular bundles. A similar situation is found in most assimilatory stems. In dry climates a reduction in distance from the bundles to the green cells is advantageous, and hereditary characters involving such a reduction are selected by nature. Thus in *Geranium sanguineum* the breadth of the leaf segments and the distance to the green cells from the bundles decrease from maritime to continental races (Böcher & Lewis 1962).

Intercellular spaces handicap diffusion through the mesophyll in the plane of the blade and this resistance to flow is clearly particularly great in spongy parenchyma. In the assimilatory stems the spongy type is absent and in most species the green cells are placed close together, the intercellular spaces being very narrow and short (see e.g. *Discaria, Colletia, Cassia, Prosopis sericantha*). In many cases radial rows of elongate palisade cells issue from cells which are endodermal or are situated very near the conducting tissues in the stele. Such radiating rows are easy pathways for water or food materials.

From the descriptions it appears that six species have small green leaves. Three of these are dorsiventral and three isolateral. In the dorsiventral leaves the palisade tissue is well developed while the spongy parenchyma is reduced.

Going through our material it appears that the distance from the conducting to the photosynthetic tissues is short in most species. In *Verbena scoparia, Psila,* and *Aphyllocladus* a typical endodermis is inserted between the two types of tissues. In *Cassia* and *Discaria* the distances are longer due to the parenchyma occurring in the outer part of the stele. In *Verbena scoparia* the transfer appears to be easy in young stems but more difficult in older ones except perhaps for water which may flow in the walls of the thick lignified cells which form a sheath inside the endodermis. A similar sheath of mechanical cells occurs in *Stillingia* but is here more frequently interrupted by living parenchyma cells and laticifers. The role of the laticifers in the water economy of this species is unknown, but it is worth-while calling to mind the very close connections which exist between the green cortex cells and the laticifers (Fig. 3) as well as between the abaxial leaf palisade cells and the mixed tissue of parenchyma and laticifers (Plate IIb).

The cylindrical arrangement of the green palisade cells surrounding sheath cells (sometimes clearly endodermal) and centrally placed conducting tissues has a striking resemblance to the structure in leaves of species wich have a photosynthesis of the C_4-type. However, the sheath cells in the stems of the apophyllous species are not provided with larger chloroplasts and no experiments are available which might demonstrate the occurrence of a deviating type of photosynthesis. So far, *Panicum turgidum* Forsk., described by Volkens (1887, p. 149), may be the only apophyllous species which has a stem structure suggesting an occurrence of the C_4-type of photosynthesis.

Characters enabling water absorbtion and secretion

Without experimental evidence it is often impossible to estimate whether water may be released or taken up by epidermis cells, trichomes, or structures which resemble hydathodes. Considering, however, that many plants absorb water through trichomes and nodes as well as by epidermis cells placed above middle veins in leaves (Volkens 1887, Spalding 1906, Zamfirescu 1931, Gessner 1956), we may shortly summarize some observations which may be of interest in future discussions. As xerophytes usually have a high osmotic pressure, they will during periods without water stress take up so much water that some of it is secreted. A water exudation through ectodesmata in young stems and leaves was shortly discussed above. Tips of scale leaves may contain tracheary elements, even wide water storing tracheoid cells which sometimes are surrounded by large elongate cells forming a bundle sheath (Fig. 13). During periods of growth these tips may function as hydathodes. Later the scale leaf tips are shed and the scar covered by an abcission cork layer. In other cases where trichomes are involved we may assume that water may be secreted under moist conditions but absorbed during dry periods. Trichomes which are ascribed to an absorbing function are found in furrows on the surface of leaves (e.g. Fig. 44 a, 45) where adjoining hypodermal or mesophyll cells are developed as a localized water storage tissue. In species with opposite adjoining leaf bases two opposite stem furrows are formed which lead water down to the next node where it may be absorbed by trichomes or epidermis cells in the axils if not already by the hairs situated in the furrows (see pp. 48 and 92).

The occurrence of small foliage leaves in a number of the species discussed in the present paper should not be looked upon as a non-xeromorphic character. Such leaves are from an anatomical point of view mesomorphic, but they are usually shed at an early stage and are probably very important during periods of growth where water is available and effectively taken up due to the high osmotic pressure of the root hair cells. During such periods a rapid transpiration may be necessary and substitutes a water secretion from scale leaf scars or glands in species without green leaves.

The water which is taken up contains mineral elements of which many occur in excess and are accumulated in crystals. Leaves which are shed may, therefore, as well as flowers etc. be of importance also for the excretion of superfluous salts because they often contain great amounts of crystals, mostly calcium oxalate crystals (cp. p. 76).

C. Evolutionary considerations

A summary of morphological and anatomical characters for the individual species treated in the present paper would in all cases include dominating photosynthetic activity of the stem, while such activity would be slight or missing in the leaves. The change from dominating leaf photosynthesis to dominating stem photosynthesis does not in itself involve any adaptation to xeric conditions, but this change is usually accompanied by changes in a number of characters which probably are of selective

value in dry habitats. First and foremost the transpiring surface is markedly reduced by early shedding of leaves or by suppressing of foliage leaves. Next the pathways for water and food materials from the vascular system to and from the assimilatory tissues are much shorter in apophyllous species.

Still, stem-assimilatory species are a priori neither xerophytes nor xeromorphic. Apophyllous species of the genus *Equisetum* are mesophytes or limnophytes. But the apophyllous structure may often represent final, true xerophytic stages in evolutionary lines which were initiated with mesophytic plants. Several such lines can be traced. First, the apophyllous structure developed in two ways which might be called the succulent and non-succulent. Next the development took place independently in very different systematic groups. While succulent apophyllous plants evolved in *Caryophyllales, Euphorbiales* and *Gentianales* and a few others, the non-succulent xeromorphic apophyllous type emerged in many groups, ancient ones as *Ephedrales,* as well as later ones such as the ten families included in our papers and further e.g. *Apiaceae, Polygonaceae, Casuarinaceae, Asparagaceae,* and *Restionaceae.*

According to Zohary (1961 : 205) apophyllous broom-like forms are more common in the Mediterranean and sub-humid regions than in deserts. Some of the genera have representatives both in deserts and at the Mediterranean. On the other hand, apophyllous plants under humid conditions behave variously as to transpiration rate, while those occurring in the Sahara have a lower rate of transpiration than fully-leaved species (Leyerer 1956).

The three types of non-succulent apophyllous species which are mentioned in the present paper represent a subdivision of this life form in (1) plants with continuous cortical chlorenchyma, (2) non-furrowed plants with interrupted cortex chlorenchyma, and (3) plants with furrowed stem and chlorenchyma connected with the furrows. From an evolutionary point of view it is interesting to see that all three types are developed in *Fabales,* thus the first in *Cassia,* the second in *Acacia continua* (Cannon 1921 fig. 15), *Prosopidastrum, Ramorina girolae* (O'Donell 1939), and the third in *Corallospartium* (cp. Slade 1952) and *Retama raetam* (Evenari 1938 fig. 6) or *Genista* e.g. *G. aetnensis.* A similar evolution towards all three types is found in *Asterales* viz. (1) in *Tetradymia* (Böcher 1971), (2) in *Psila,* and (3) in *Aphyllocladus.*

Besides the three life form subtypes a forth subtype occurs in the two systematic groups, viz. the flattened subtype characterized by flattening of the stem to cladodes which resemble isolateral leaves or by development of flat stem wings, also with isolateral structure. In *Fabales* cladodes are described in *Carmichaelia* by Slade (1952) and stem wings occur in European montane *Genista sagittalis.* In *Asterales* the genus *Baccharis* contains a striking example of the winged type in the South American *B. articulata.* In most cases the flattened subtype is perhaps more mesophytic than the terete or furrowed ones.

Considering the four different subtypes, all represented in the two orders, it is evident that the approach to an apophyllous life form was different within the systematic groups, but that four evolutionary trends in both groups led to the same subtypes.

These may roughly be characterized as character combinations by which the supporting and assimilatory tissues are arranged in four different ways.

A study of the epidermal and cortical characters found in the six species mentioned above as examples of the first three subtypes (Table 1) shows clearly how different these species are, not only if we compare the pairs belonging to the same subtype, but also if we make a comparison of the three members of the same systematic group. It is striking, however, that apart from the absence and presence of ducts, the difference between the two species of subtype (3) is very modest, a fact which confirms how difficult it is to use morphological similarity in taxonomical considerations.

The characters mentioned in Table 1 are probably to a great extent vicarious. A thick hair cover in *Tetradymia* may be vicarious to an epicuticular wax cover in

TABLE 1

	Subtypes of xeromorphic apophyllous plants (cp. p. 131).		
	1	2	3
	Cassia aphylla	*Prosopidastrum globosum*	*Corallospartium crassicaule*
	Epicuticular wax		
	Cuticular layer thick	Cuticular layer thick, peeling off	Cuticular layer thick on ridges
	Narrow extra front cavities	Front cavities large, not protruding. Outer ledges well-developed	Furrows with stomata and hair cover
Fabales	Small front cavities		
	Water contents in thick hypodermal cell walls	Multiple epidermis	
	Narrow intercellular spaces		
	Endodermis not very distinct	Endodermis not very distinct, without suberized walls	Endodermis distinct No ducts
	Tetradymia axillaris	*Psila spartioides*	*Aphyllocladus spartioides*
	Thick whitish hair cover		
	Thick cuticular layer	Cuticular layer	Thick cuticular layer on ridges
	Shallow extra front cavities	Vesicular protruding front cavities	Furrows with stomata and hair cover
	Front cavities	Interior ledges prominent	
Asterales	Wide intercellular spaces and cavities	Interior walls of epidermal cells cutinized	
	Bundle sheaths in young stems probably corresponding to an endodermis	Endodermis distinct, its cell walls suberized, passage cells present	Endodermis not distinct
		Ducts present	Ducts present

Cassia, and furrows in the stem may be vicarious to well-developed front cavities. In *Tetradymia* the many intercellular spaces in the stem represent a non-xeromorphic character which, however, may be possible in a xerophyte because they occur in combination with a thick whitish hair cover, front cavities, and a thick cuticular layer, thus a threefold anatomical protection against water loss.

As characters seem to be able to substitute one another, it becomes evident that the same level of adaptation can be reached by different character combinations. Still, some of the characters are clearly particularly important and become superior. Such characters may be morphological as e.g. shrubby habit, apophyllous, and deep-rooting, or anatomical as e.g. thick cuticular layer, protection of stomata, reduction of pathways for water etc. The superior characters are those which characterize the life forms.

Subject index

In the present paper a number of species have been treated in a monographic way. Among the many characters are some which are not xeromorphic or characteristic of xerophytes although found in xerophytes. Such characters are mostly dealt with rather superficially, still they are thought to be of some importance for the general understanding of what has been discussed or touched on in the paper. In a few cases, e.g. the treatise of the extra-floral nectaries, the observations have led to discussions wich may be of more general interest. The wall structure of the secretory cells are particularly relevant in connection with the many other observations on epidermal cell wall structures. The following alphabetical index is not complete. Page numbers in italics indicate illustrations.

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PLATES

Plate I

Stillingia patagonica. Surface of stem as seen in scanning electron microscope (SEM). — a–b. Surface showing foveae, at arrow stomatal pore (a × 100, b × 520). — c. Deep fovea with granulated surface. Wax cover on surface regularly cracking (× 2000). — d. Front cavity of stomatal pore situated in bottom of elongate fovea (× 2100).

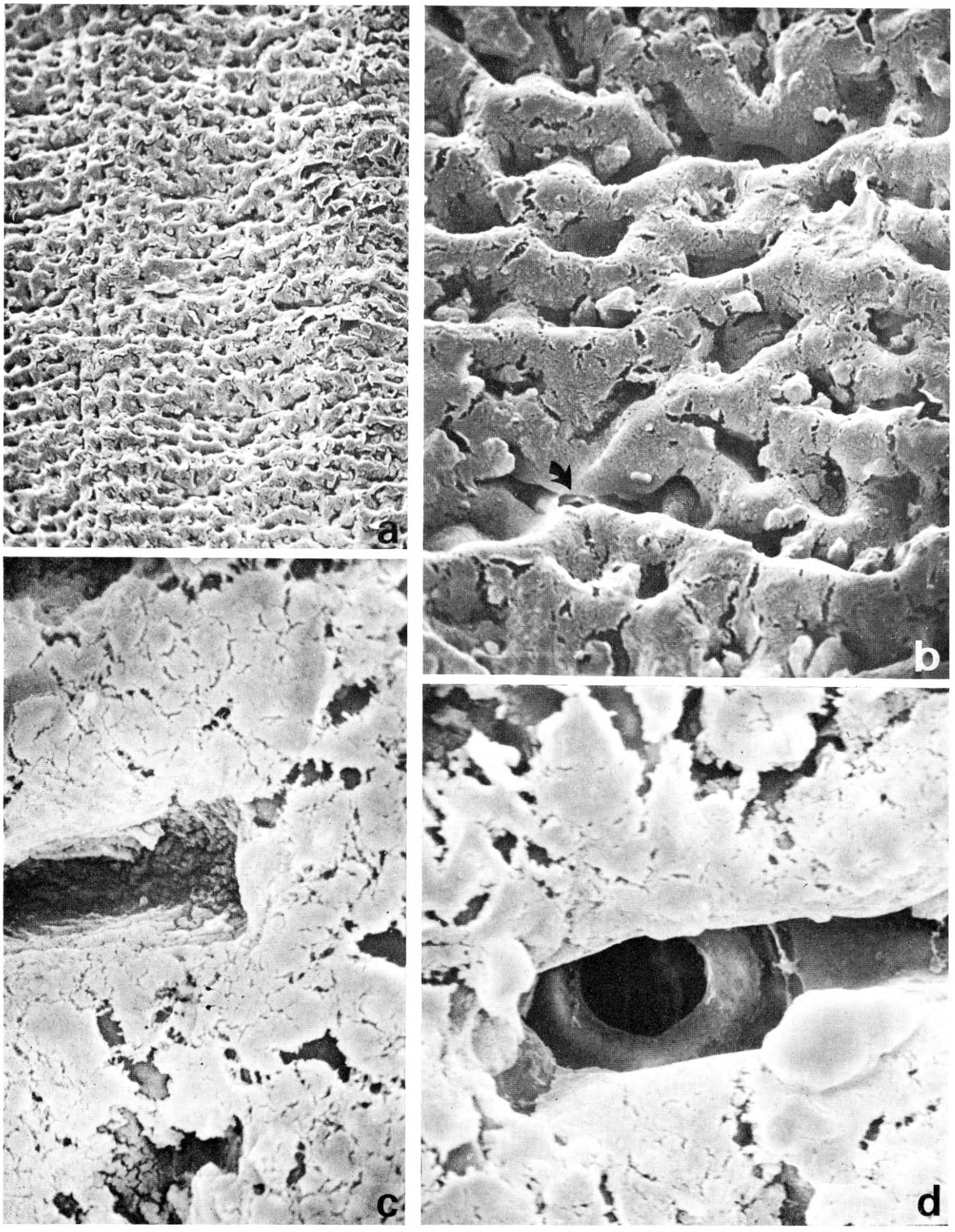
a
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Plate II

Stillingia patagonica. a. Margin of leaf blade. Epidermis cells on adaxial side with densely spaced cuticular ridges. Hypodermis well developed on abaxial side. Behind green cells on this side a complex laticiferous tissue which covers the phloem (× 320). — b–d. Secretory tissue bordering cavity in extra-floral nectarium. c. Youngest stage with small cuticular papillae and initial phase of widening of outer walls separating the cells. b. and d. Older stages, in (d) showing broad cutinized walls between the outer parts of the cells and broader papillae traversed by micro-channels. Outside transverse walls small cavities (channels) e.g. at arrow. (Safranin-Fast green staining and interference contrast, × 2000).

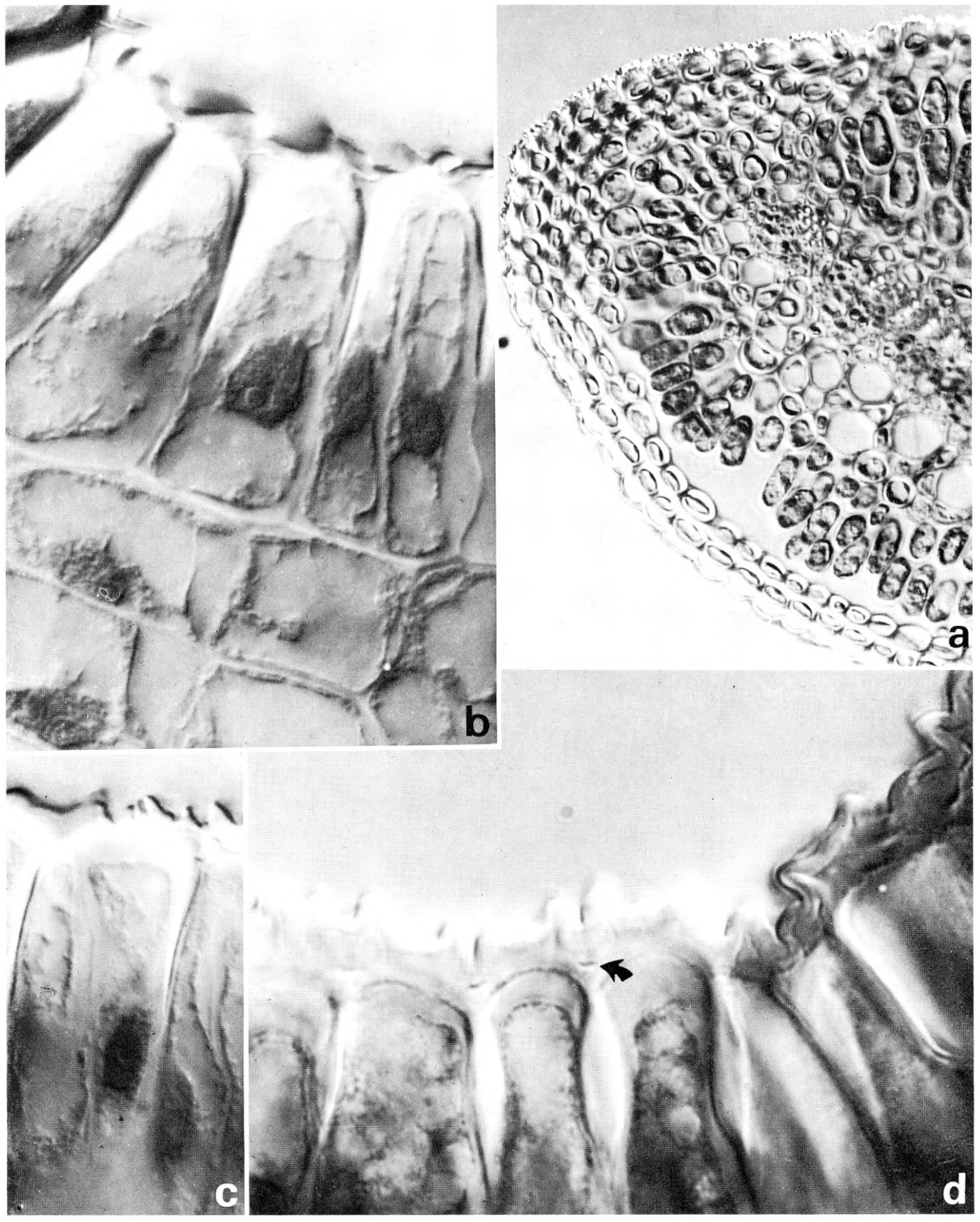
a
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Plate III

Cassia aphylla aggr. a. Transverse section of young stem giving outline of layers: Epidermis, hypodermis, palisade (two interior layers with dark cell contents), fiber strands (outside groups of primary phloem), phloem parenchyma, phloem, cambium, xylem and pith parenchyma (some cells containing dark substances, tannin) (× 200). — b. Thick section showing outer palisade cells arranged in a substomatal area with wider intercellular spaces. Four subsidiary cells (light) on both sides of guard cells (× 320). — c. Longisection showing 5–6 subsidiary cells (dark) and small hypodermal substomatal chamber due to Y-shaped cell connected with 2–3 subsidiary cells. Thick-walled hypodermal cells continuing in group of similar cells inserted between outer palisade cells (× 800). — d. Crystal cells lining fiber strand (interference contrast, × 320). — e. *C. crassiramea*. Transverse section of xylem in polarized light. Biseriate ray, each cell with a crystal except the short cells at arrow which on both sides continue in a layer of short cells resembling a cambial layer. The position of the functioning cambial layer is indicated with asterisks (× 500).

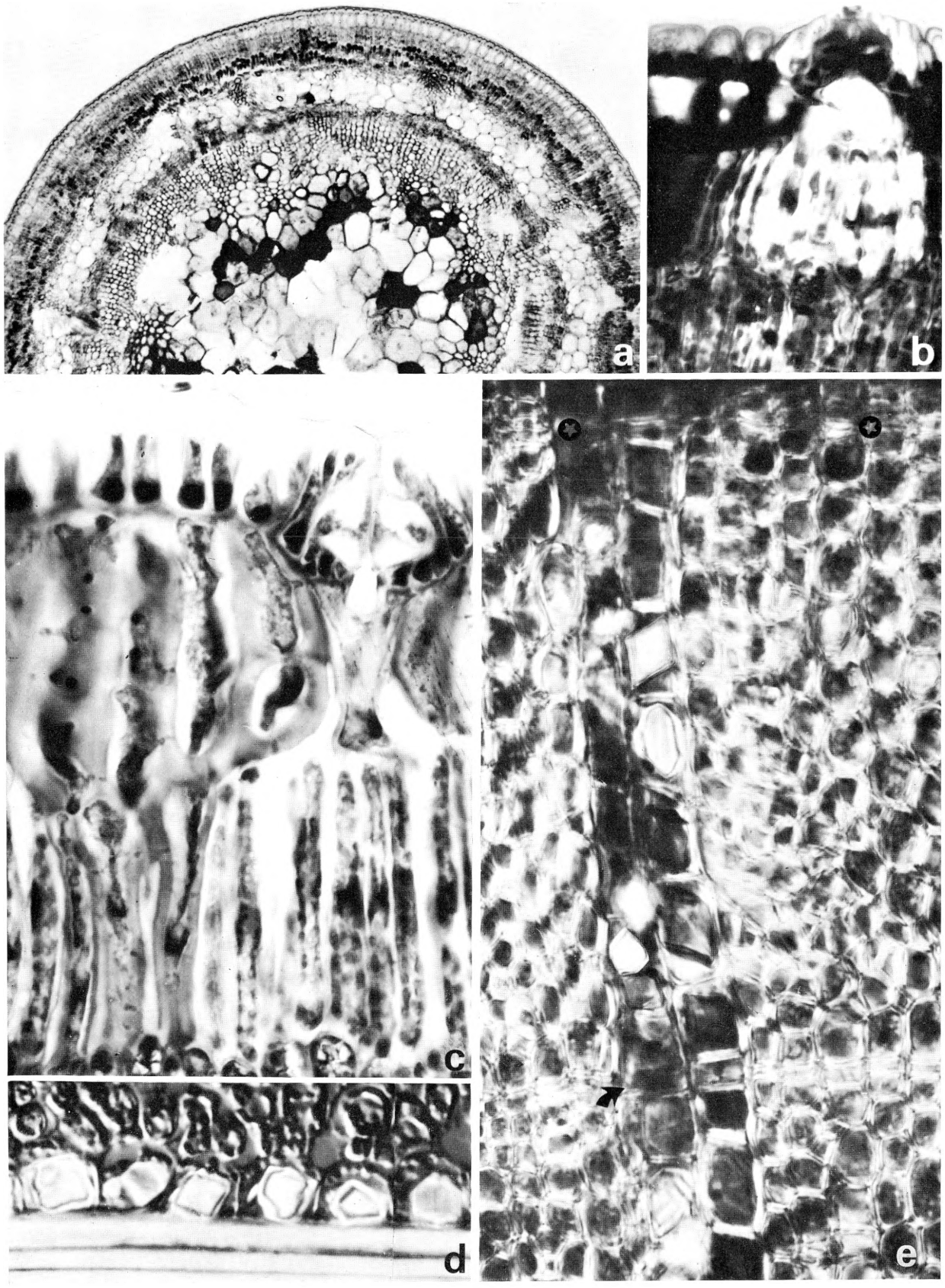
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PLATE IV

Cassia aphylla aggr. — a–b. Stomatal openings as seen from outside (a) and from inside (b), (× 500). In (a) numerous wax scales on surface (SEM micrograph), in (b) marked difference between first and later formed epidermal walls. — c. SEM micrograph of sheltered area outside front cavity as seen from outside, wax covering cracked (× 2150). — d. Transverse section of stomatal apparatus and subsidiary cells stained with Sudan IV. Cellulose walls in guard cells and some remaining wax in sheltered area outside front cavity birefringent (× 2000).

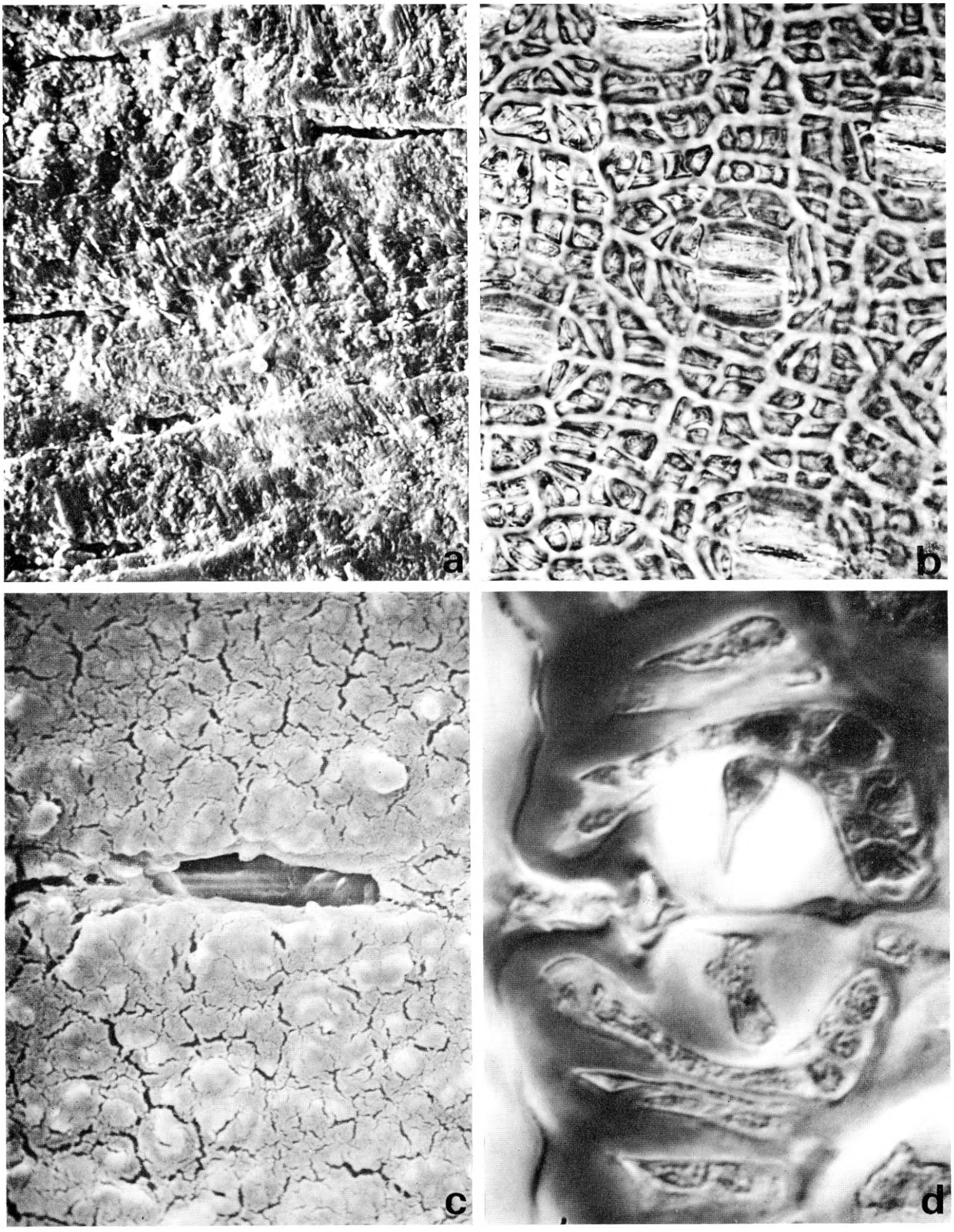
a
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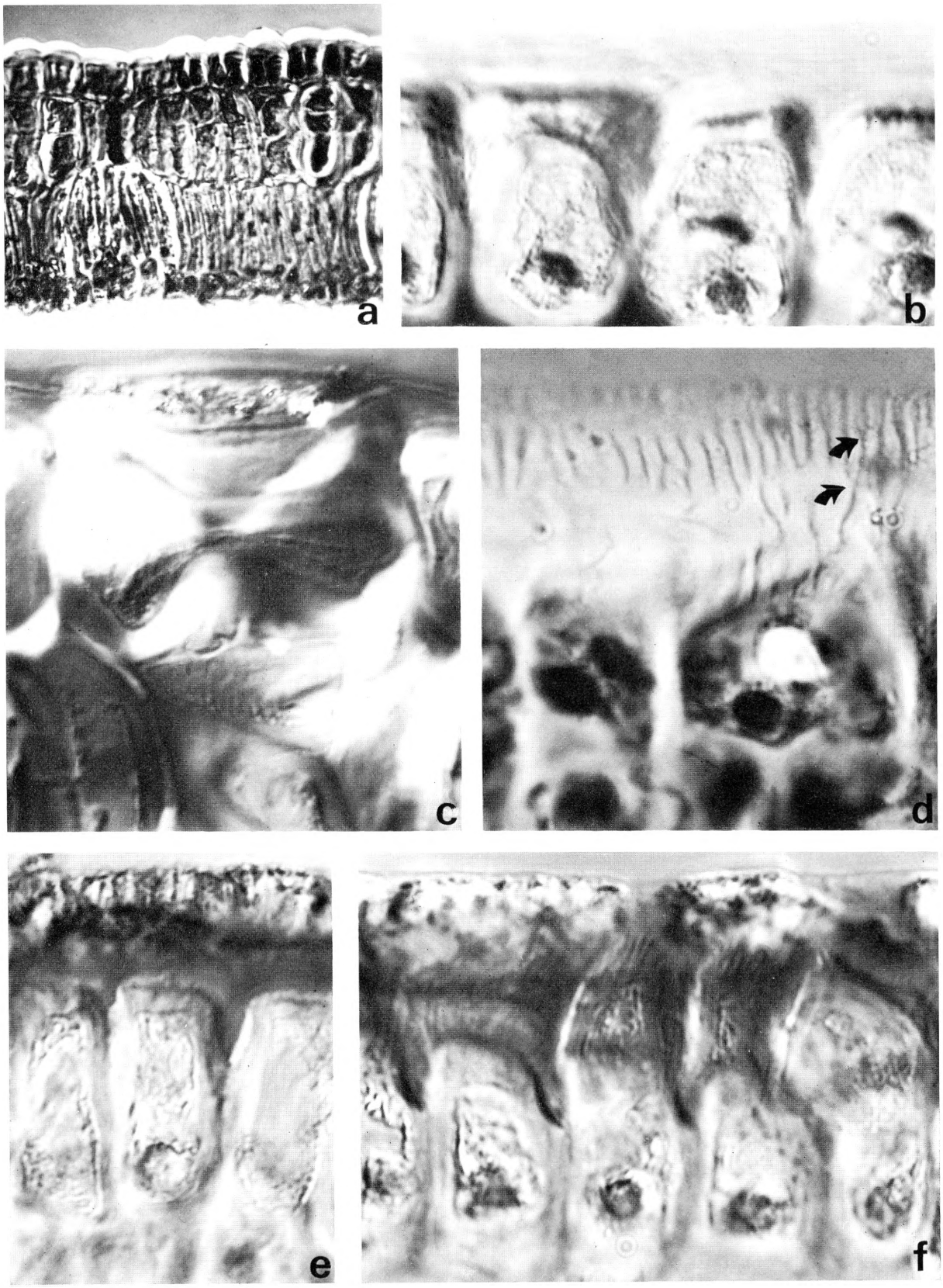
Plate V

Cassia aphylla aggr. a. *C. rigida*, d. *C. crassiramea*, b, c, e, f. *C. aphylla* (a × 320, b–f × 2000, all interference contrast). a. Epidermis with long cuticular flanges below primary walls and short flanges below secondary walls. Dome shaped area in outer palisade layer is situated below narrow substomatal space (out of focus), cf. Plate IIIb. — b. Epidermal cells showing lamellation in outer walls and radiating structures (micro-channels), cell nucleus recently divided in two in cells on the right. — c. Longisection of stomatal pore showing shape of guard cell protoplast, some wax is showing up in the depression above the front cavity. — d. Oblique transverse (tangential) section through epidermis showing system of micro-channels which branch twice (arrows). One birefringent crystal near dark nucleus. — e–f. Material stained with Sudan IV showing cuticular layer and flanges and birefringent wax pattern externally, in (f) several micro-channels.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f

PLATE VI

Cassia aphylla aggr. (*C. rigida*). a. Paradermal section of substomatal chamber surrounded by 8 narrow hypodermal cells. — b. Thick-walled hypodermal cells in cross section of stem. The lefthand cell divided into three cells. Long pit canals. — c–d. Interference contrast pictures showing pit canals in cross section and possibly callose lining of canals (c) and plasmodesmata traversing middle lamella (d), arrow (× 2000).

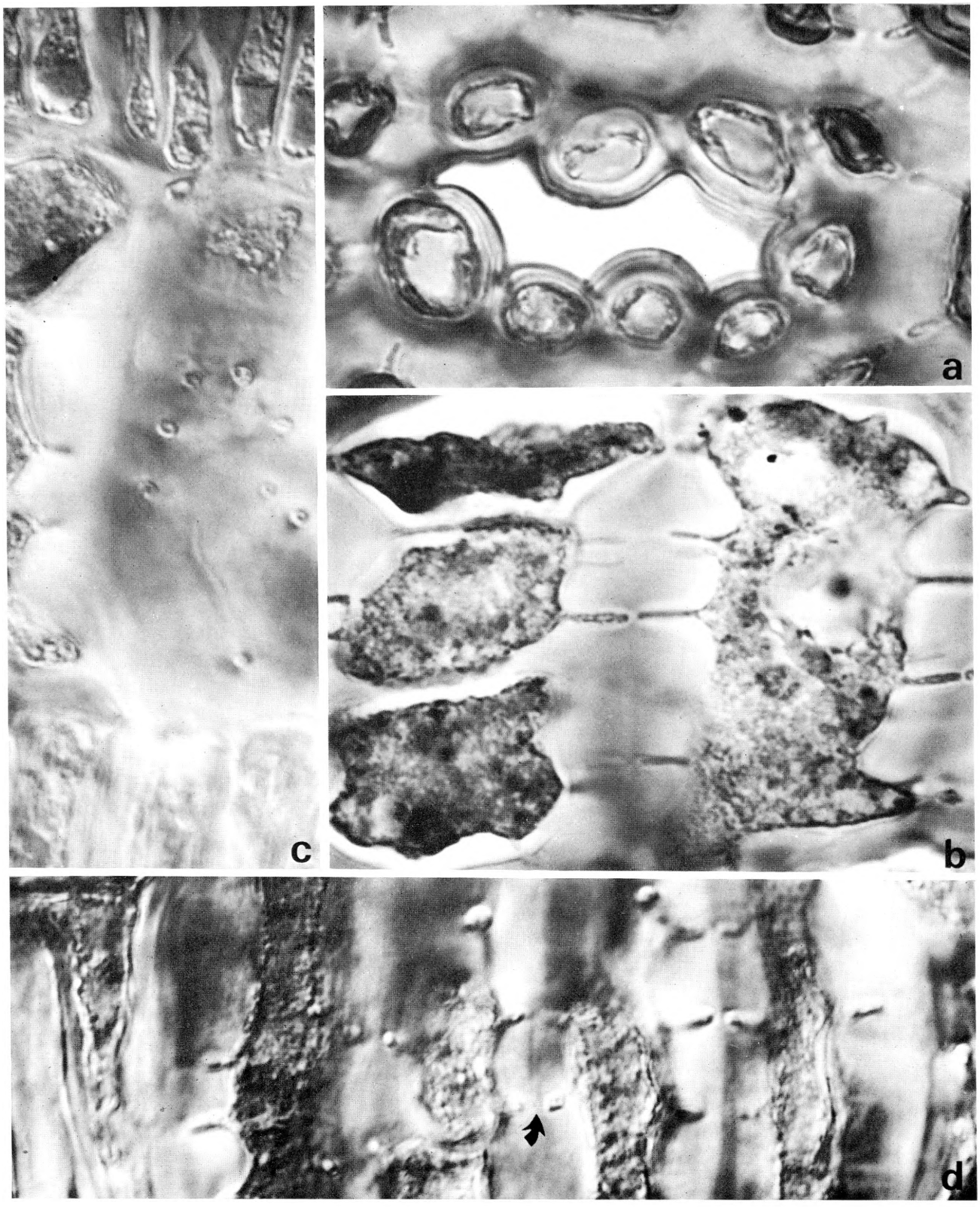
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Plate VII

Discaria articulata. a–c. SEM micrographs showing surface of stem and outer front cavities of stomatal openings, in (a) and (c) filled with fungal cells. Small scales between low ridges are probably made up of wax (a × 960, b × 1040, c × 3264). — d. Cross section of epidermis in old branch, all cells taper into a central non-cutinized canal which distally continues in numerous delicate micro-channels (Sudan IV staining, × 2000).

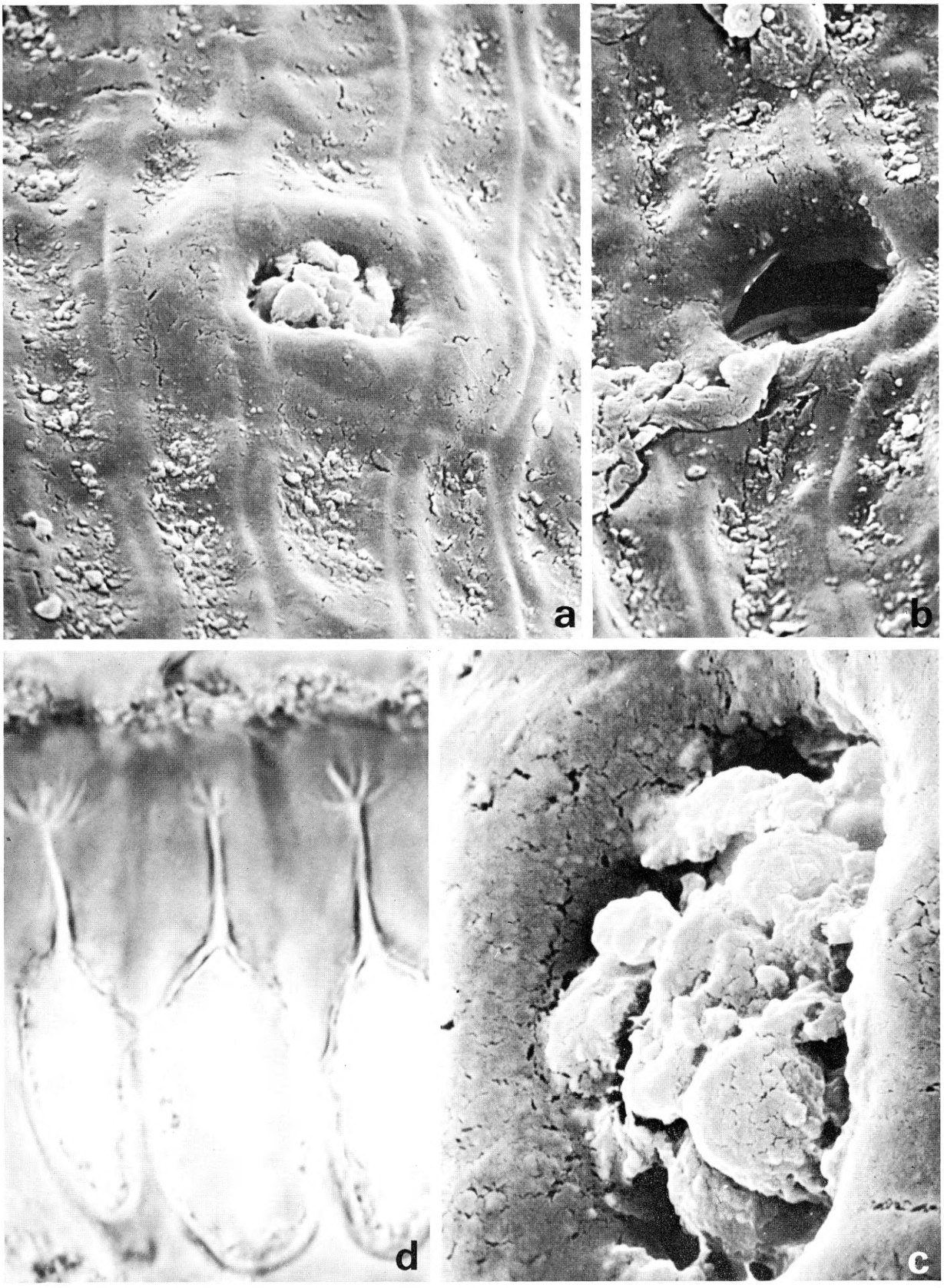
a
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Plate VIII

Discaria articulata. Cell wall degeneration in parenchyma cells near phloem fibers. — a. Cross section showing crushing of cells and deposition of brown masses, ★ remains of cell lumina. — b. Brown deposits in longitudinal section. — c. Swellings of brown cell wall, cross section. — d–e. Final stage, tangential sections showing swellings of radial walls and dissolution of transverse thin walls (× 2000).


a
b
c
d
e

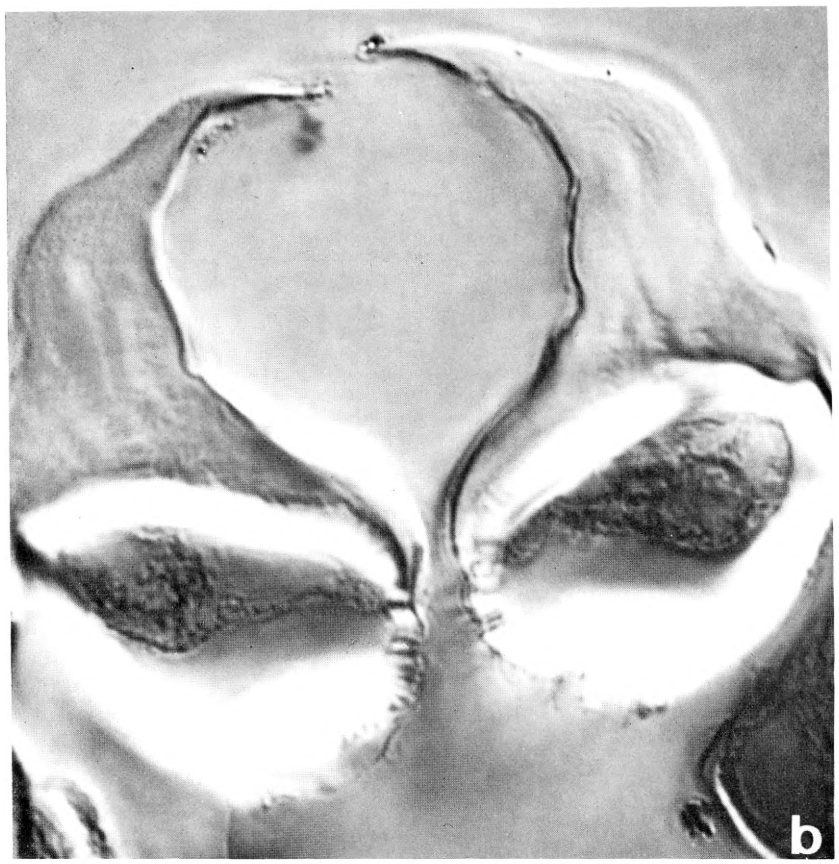
Plate IX

SEM micrographs of surface of stem in the *Fabiana denudata-viscosa* complex showing stomatal openings and dried-up varnish-like cover secreted by glandular hairs (a × 195, b × 490, c × 1850, d × 1000).


a
c
b
d

Plate X

Fabiana denudata-viscosa complex. — a. Outer part of stem with two stomata and three glandular hairs (semi-polarized light, × 500). — b. Cross section. c–d. Longisections of stomatal opening showing folds in walls facing pore (b–c) and radiating structures in the walls of the ledges (semi-polarized light, × 2000).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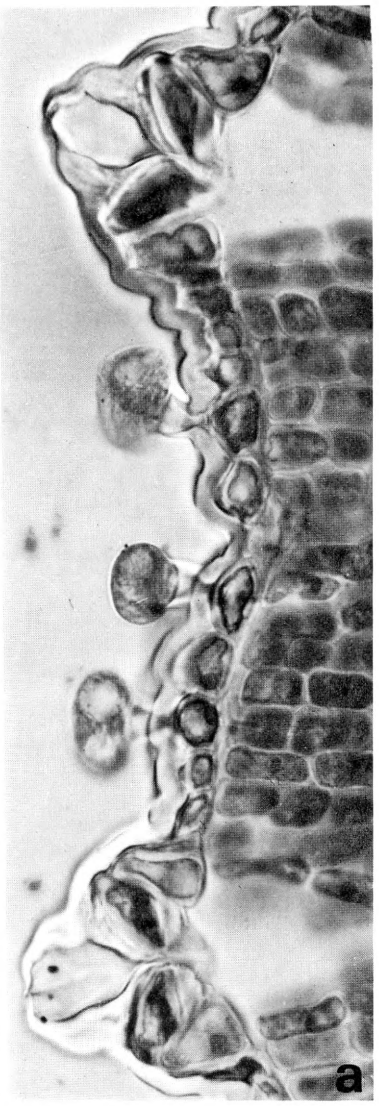
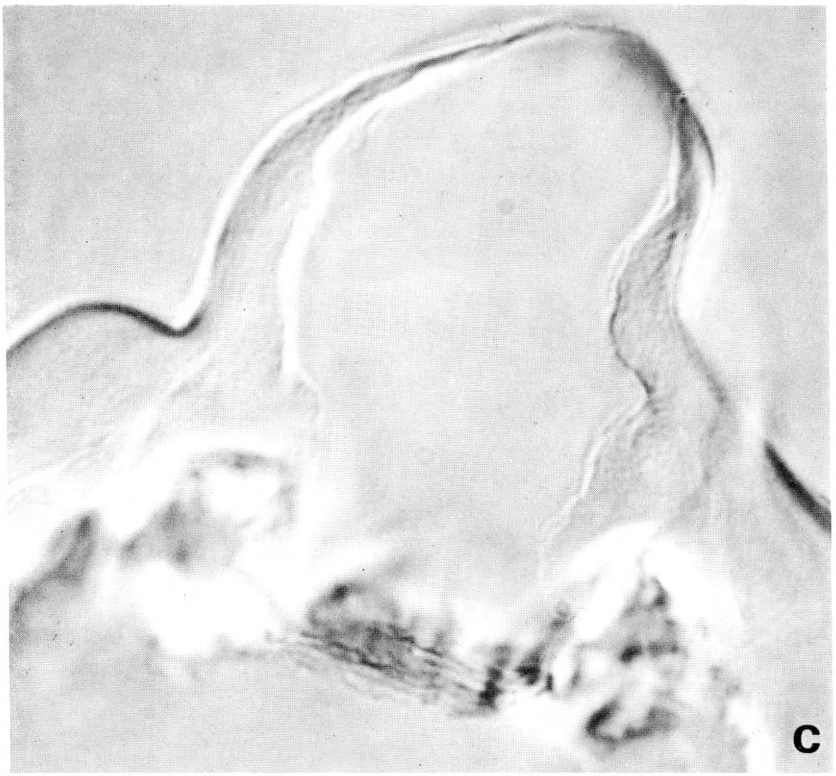

a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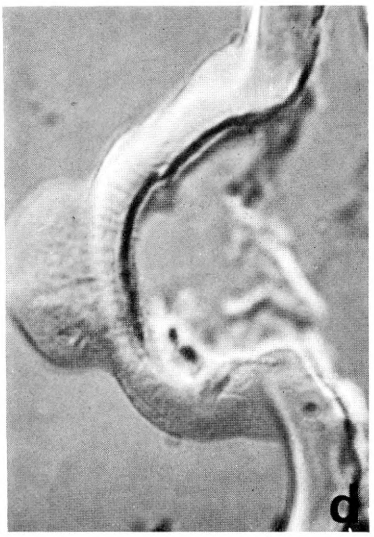
d

Plate XI

Psila spartioides. SEM micrographs of surface showing stomatal openings and wax pattern. (a × 215, b × 1066, c–d × 2150). In (a) rib covering fiber strand (cp. Fig. 32). In (c–d) small wax bridges crossing grooves around vesicular front cavities.

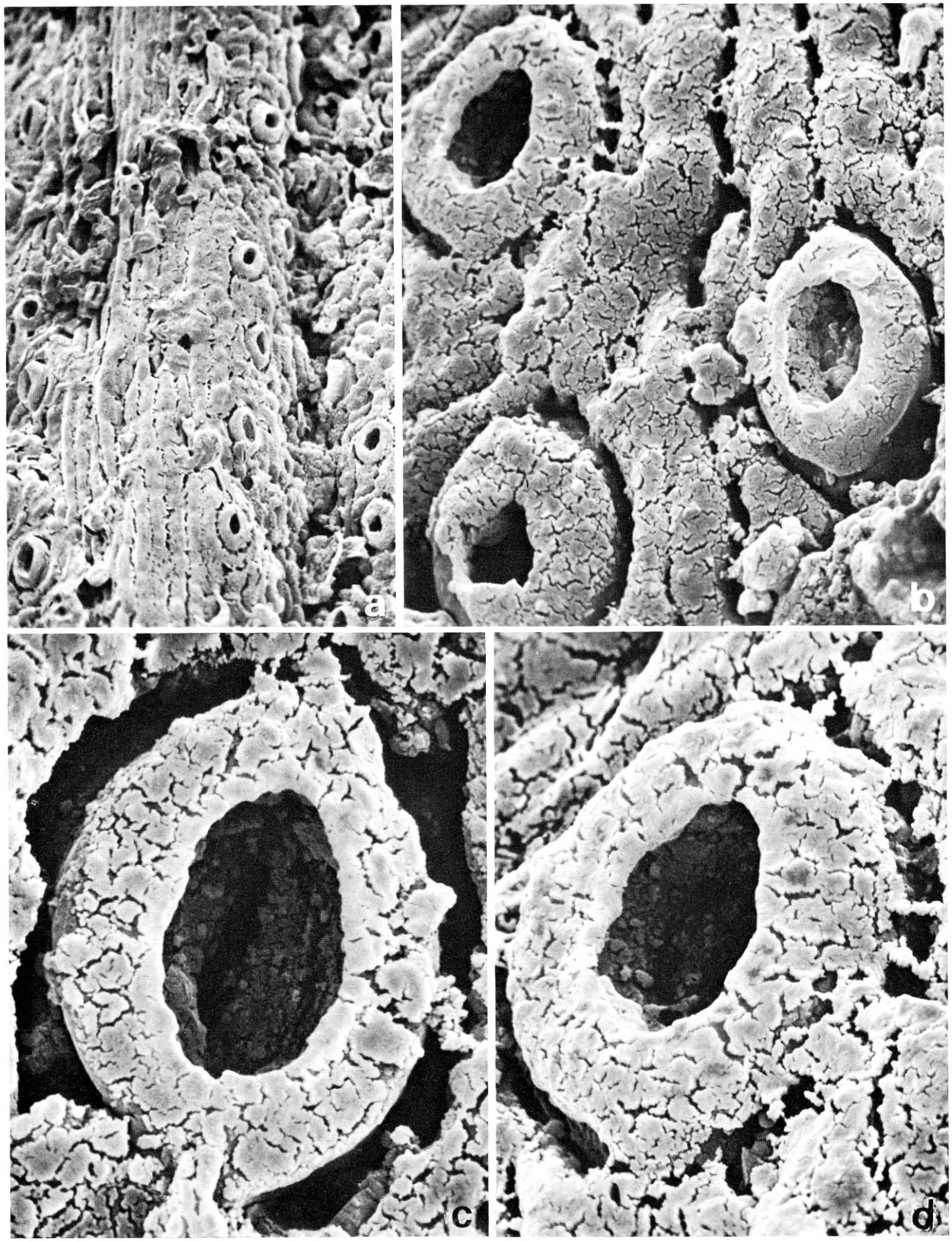
a
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Plate XII

Psila spartioides. — a–c. SEM micrographs of surface after treatment with alcohol which has removed wax (a × 195, b × 490, c × 970). A number of shrivelled glandular trichomes is seen in (a) in the middle on rib and on the left. — d–f. Cross sections and longisection (f) of guard cells (interference contrast, × 2000).

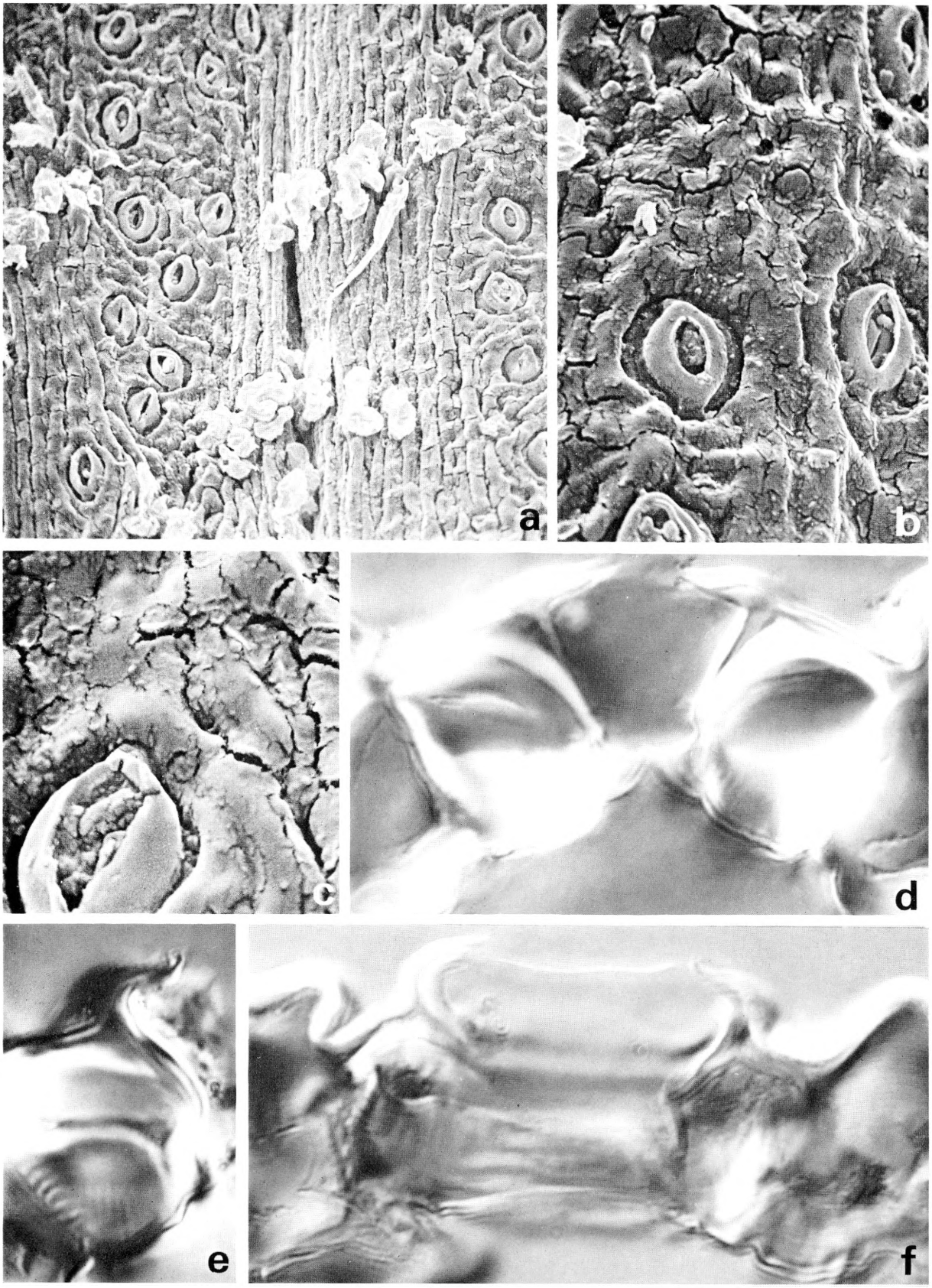
a
b
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Plate XIII

Psila retamoides. SEM micrographs of surface. — a. Oblique view showing ribs, numerous stomatal depressions and clusters of glandular hairs (× 50). — b. Surface with many stomatal depressions (× 480). — c. Depression with stomatal opening (× 1900). — d. Single opening (× 4700).


a
c
b
d

Plate XIV

Prosopidastrum globosum. — a. Cross section of stem showing position of fiber strands inside ribs, distinct layering of cortex chlorenchyma, and pith (× 40). — b–e. SEM micrographs of surface of stem; b showing three ribs and inter-rib areas with stomatal pores (× 105) — c–e showing different degrees in narrowing of pore through outer ledges (c × 525, d × 1050, e × 5250). — f. Oblique surface view of stomatal pore and surrounding cells (Sudan IV staining, × 2000).

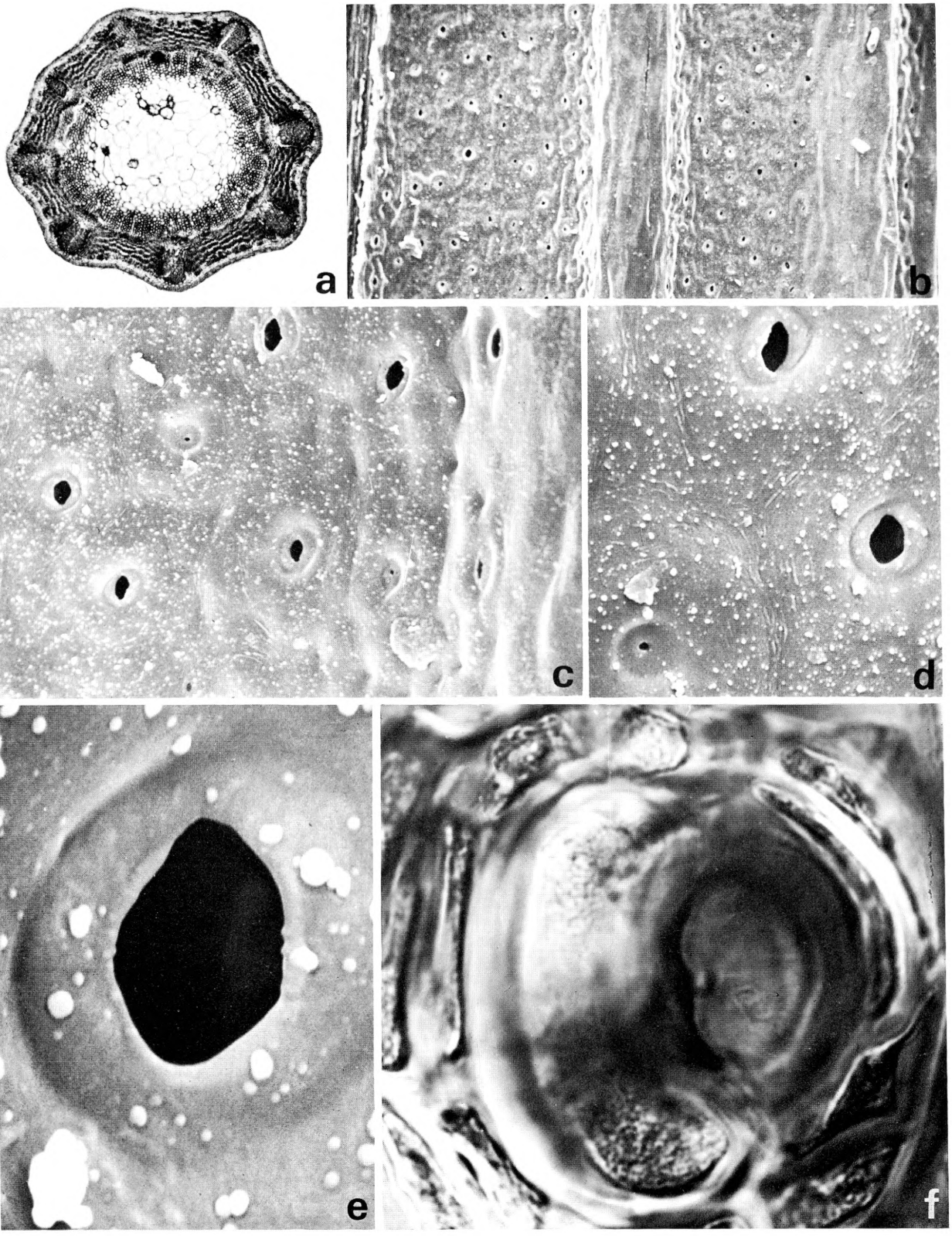
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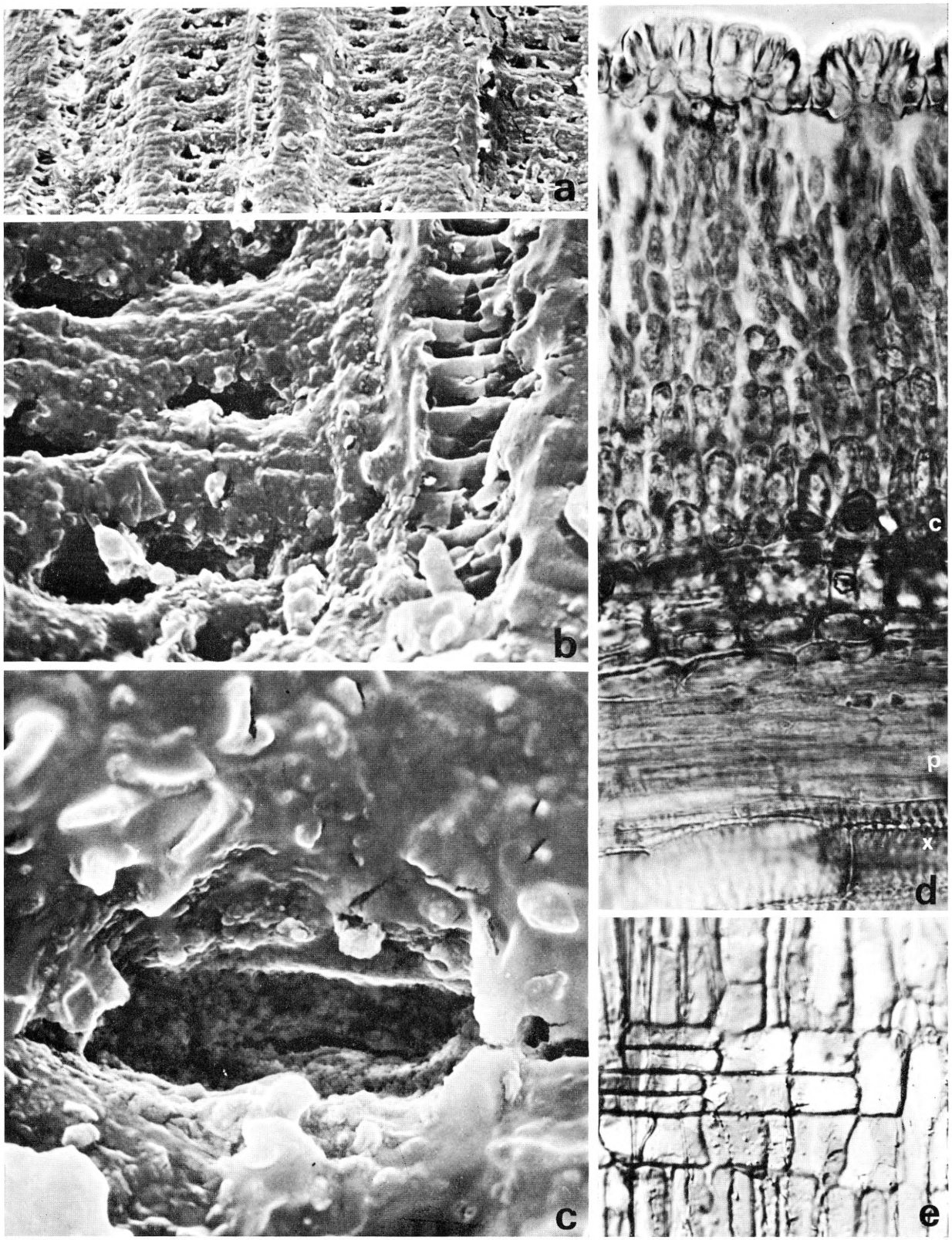
Plate XV

Prosopis sericantha. — a–c. Surface of stem, as observed in Scanning electron microscope; in (a) four ribs, in (b) margin of rib and part of inter-rib area, in (c) stomatal opening (a × 102, b × 510, c × 2100). — d. Longisection of stem, (Safranin-Fast green staining, semi-polarized light, c = cell layer with crystals behind photosynthetic cortex, p = phloem, x = xylem) (× 500). — e. Part of xylem ray (interference contrast, × 320).


a
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c
p
x
d
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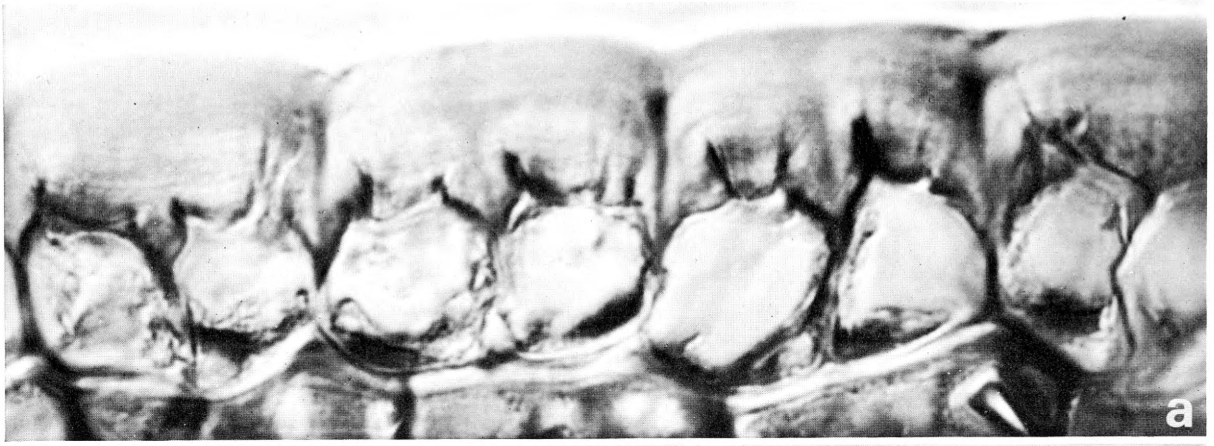
Plate XVI

Prosopis sericantha. a–b. Longisection of part of epidermis in stem showing families of two and two cells, all with lamellated thick outer walls and narrow extensions resembling ectodesmata. In (a) subepidermal layer with a triangular crystal and large oval primordial pits. In (b) stomatal openings, substomatal chamber and outer palisade cells. — c–d. Younger and somewhat older fiber cells showing cross striation (Quadruple staining, interference contrast, × 2000).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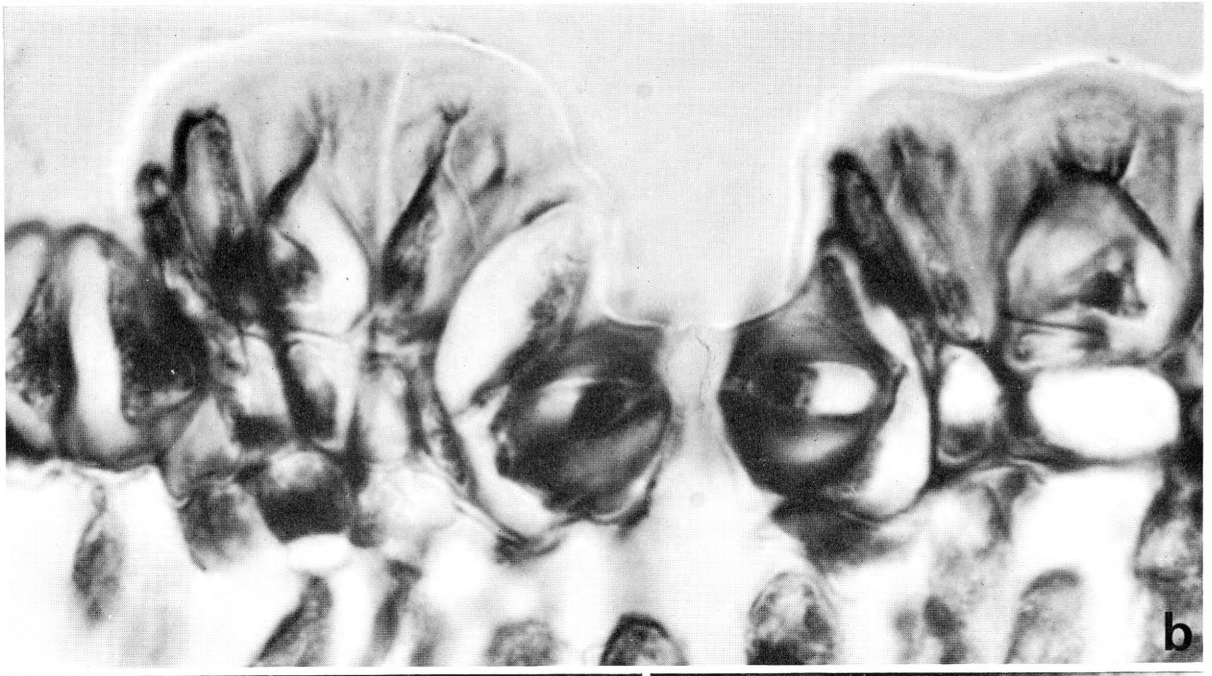
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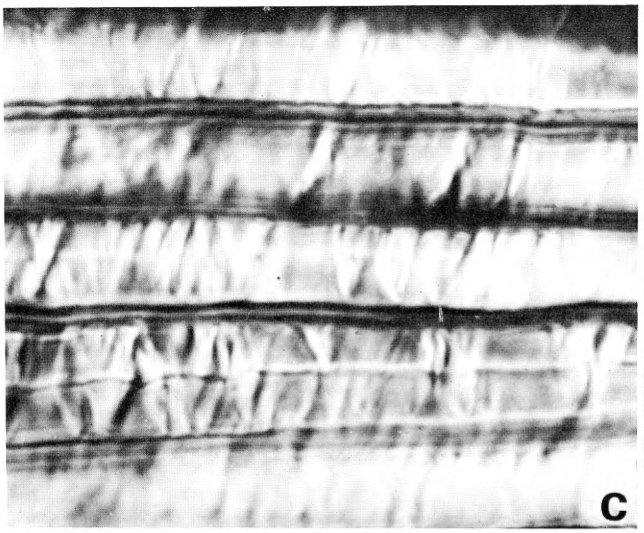
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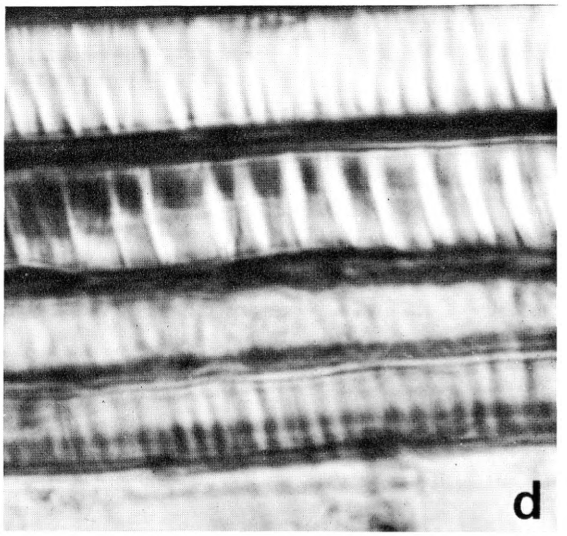
d

Plate XVII

a–c. *Junellia glauca*, d–f *Junellia* (No. 717) closely related to *J. glauca*. a–b. SEM micrographs, oblique surface view, showing depression with stomatal pore (a × 200, b × 1850). — c. Cross section of stomatal pore showing narrow fissure between thick cutinized guard cells, arrow points towards wax remains in depression outside front ledges (Sudan IV staining, semi-polarized light, × 2000). — d–e. SEM micrographs of surface showing cracks in pore in thin diaphragm produced by outer ledges (d × 530, e × 2100). — f. Cross section of stomatal pore. Guard cells larger than in typical *J. glauca*. Depression outside front cavity absent. (Sudan IV staining, interference contrast, × 2000).

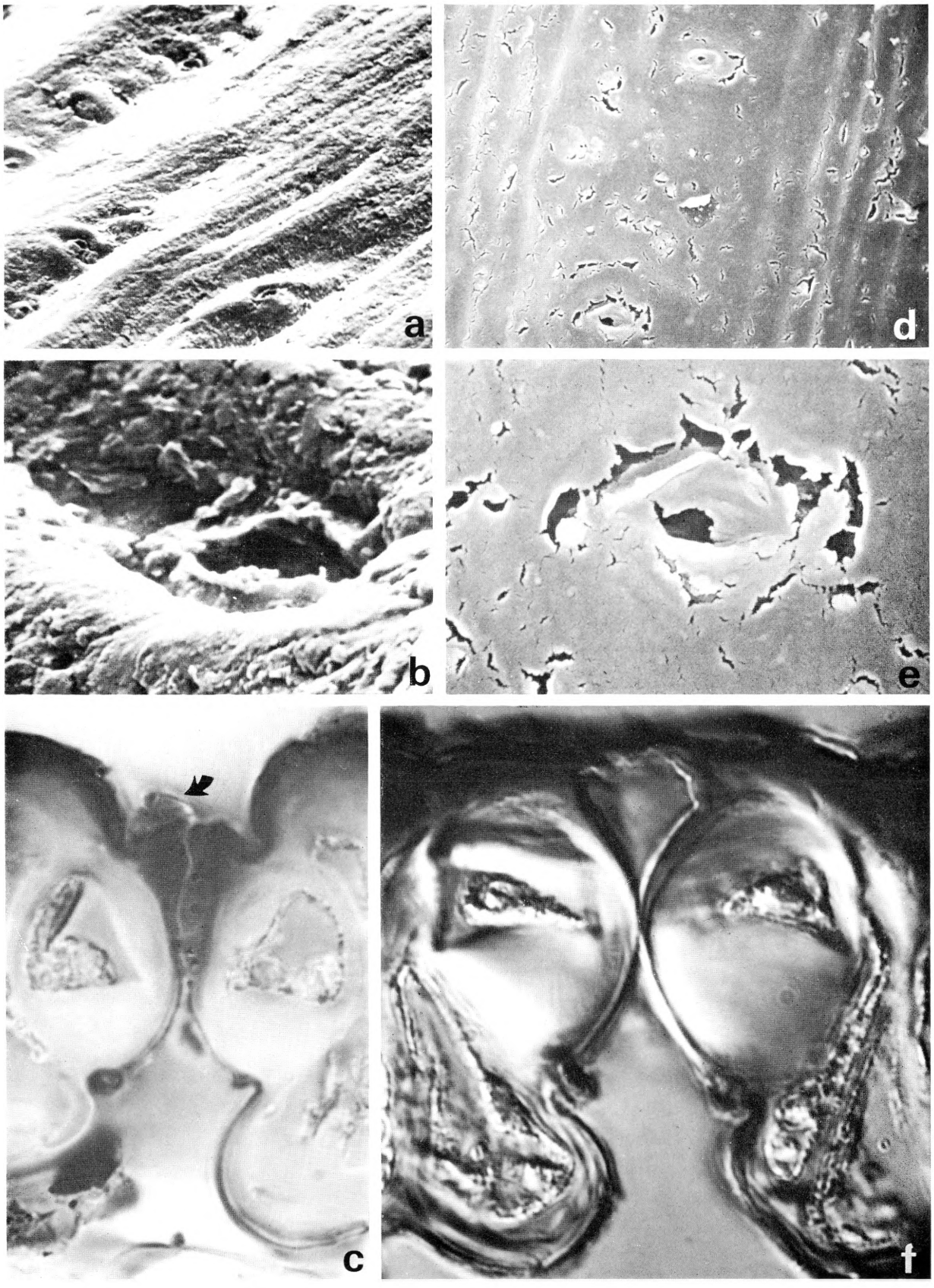
a
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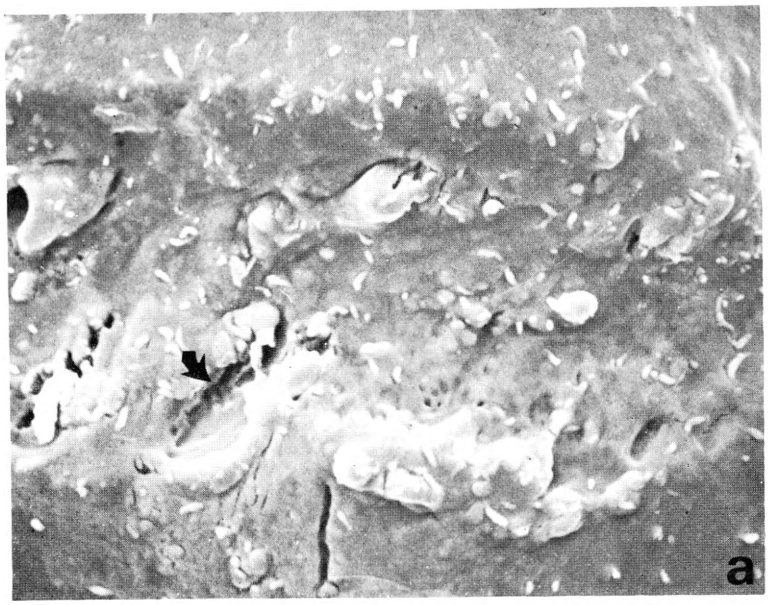
Plate XVIII

Verbena scoparia. a. and e. SEM micrographs of surface, b–c. cross sections of outer walls of epidermis cells, d. of stomatal pore. — a. Surface view of depression, arrow points towards openings with remains of wall lamellae above cuticular flange, cf. arrows in (b–c). — b–c. Outer walls of epidermis cells showing outer porous part and openings in cuticular layer outside transverse walls with remains of wall layers resembling a ladder (arrows). Radiating structures near interior part, in (c) remains of cutinized hair base (Sudan IV staining, × 2000). — d. Deeply sunken stomatal opening (Safranin-Light green, interference contrast, × 2000). — e. Stomatal opening as seen from outside (× 2000).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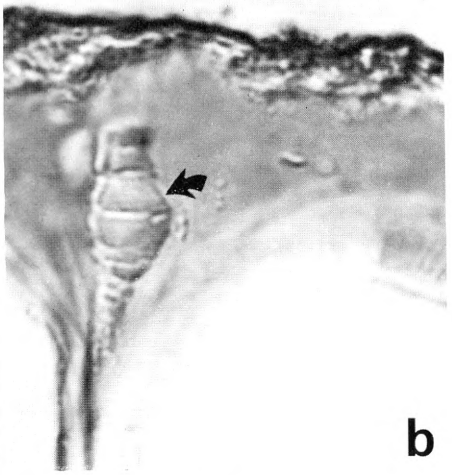
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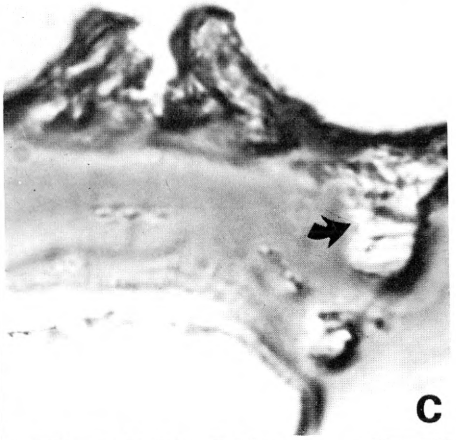
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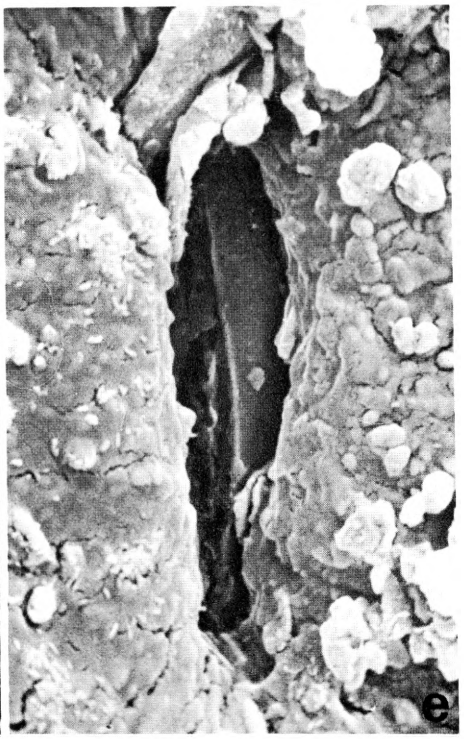
e

Plate XIX

Diostea juncea. a. Half of leaf showing size and position of extra-floral nectarium, the groove at the middle vein and the parenchyma of large cells on both sides of the middle vein (× 40). — b. Part near margin of extra-floral nectarium showing basal cells with thick cutinized (suberized) walls and secretory palisade tissue covered by a lamellated cuticle. — c. Part of epidermis with peeling off of cuticular layer. In the cells rounded or irregular whitish bodies, cp. text. Fiber cells below epidermis (Sudan IV, interference contrast, × 800). — d. SEM micrograph of stomatal openings surrounded by "rampart" (× 510) — e. View into stomatal opening towards front ledge (SEM micrograph, × 5500).

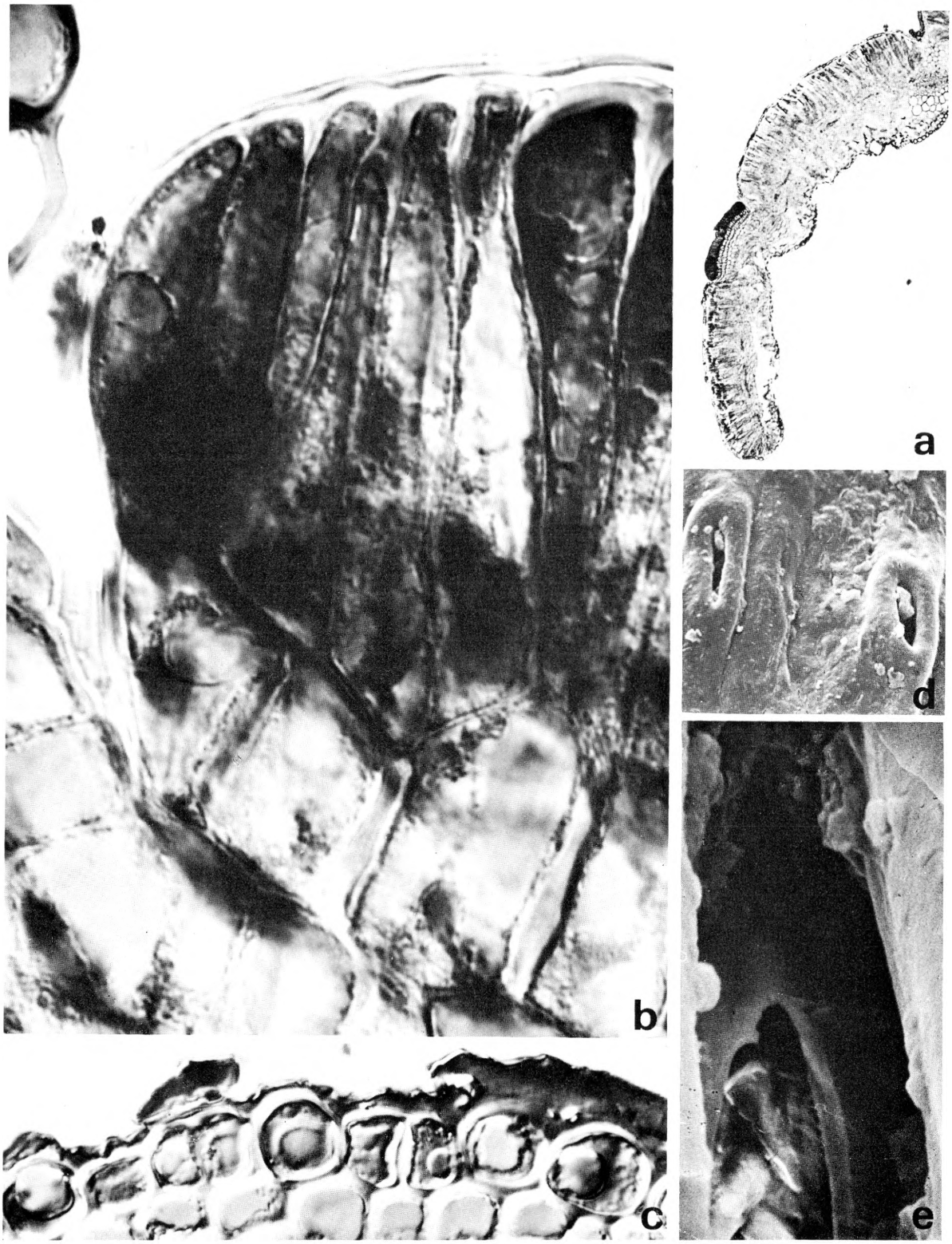
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Plate XX

Neosparton aphyllum. a–c. SEM micrographs of surface. In (a) two furrows (× 106), in (b) one furrow (× 205), in (c) one furrow, no inter-furrow area (× 1000). — d. Cross section of furrow with glandular hair in the center and stomatal opening on the right (Safranin-Fast green, × 500). — e. Stomatal opening showing central small extensions which close the pore as cogs in a cogwheel; inner ledges as well as cogs cutinized (Sudan IV staining, semi-polarized light, × 2000).

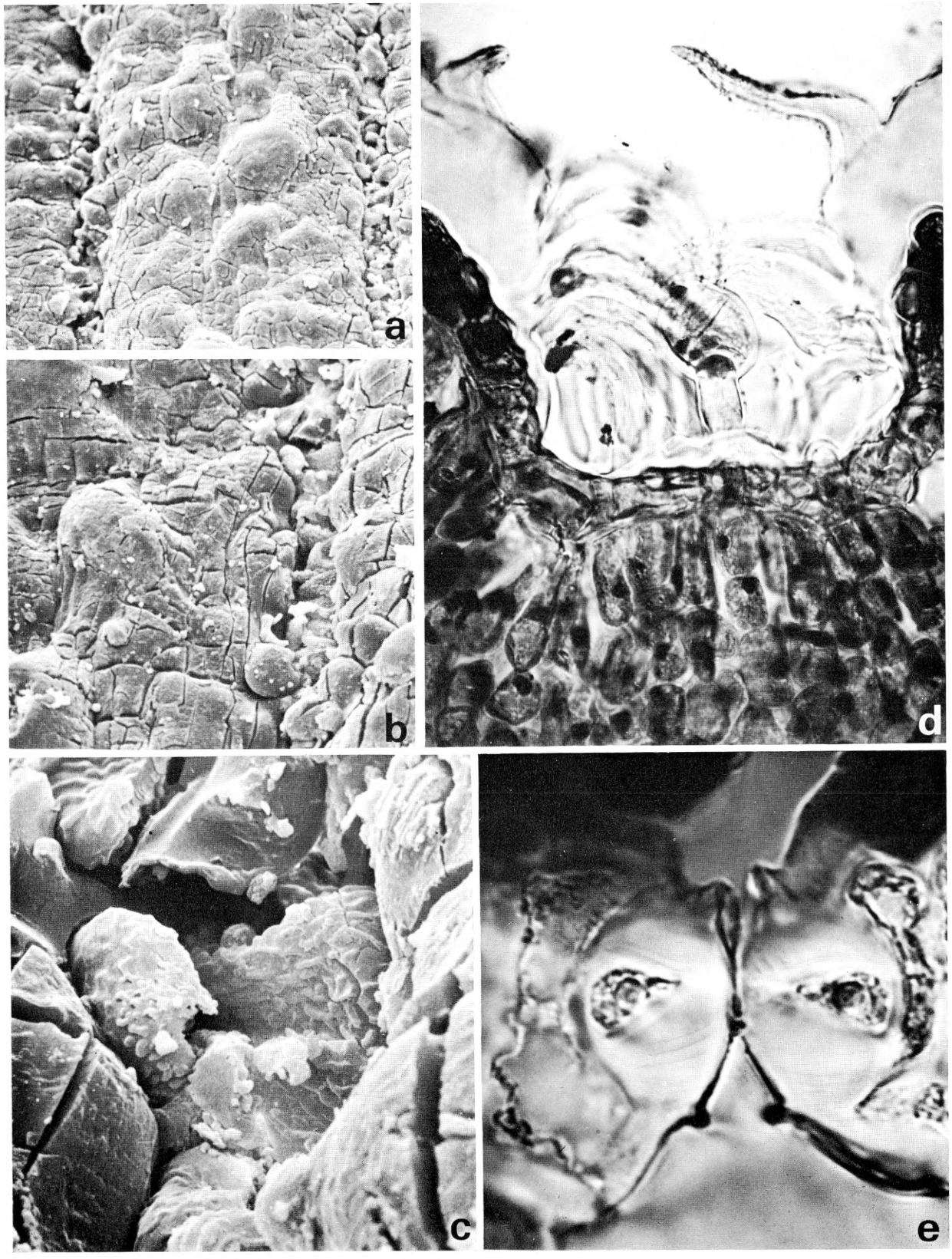
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Plate XXI

Neosparton aphyllum. Glandular hairs and extra-floral nectaria. a. Gland with beaked tip outside two upper glandular cells. — b. Extra-floral nectarium with secretory palisade tissue resting on basal cells (two separated by cutinized radial wall visible) and two large cells which continue downwards as a "root". At arrow a small pore in radial wall (Sudan IV staining, × 2000). — c–e. As (b) but showing bladders in cuticle outside radial walls in secretory palisade tissue (Safranin-Fast green staining, interference contrast, × 1400).

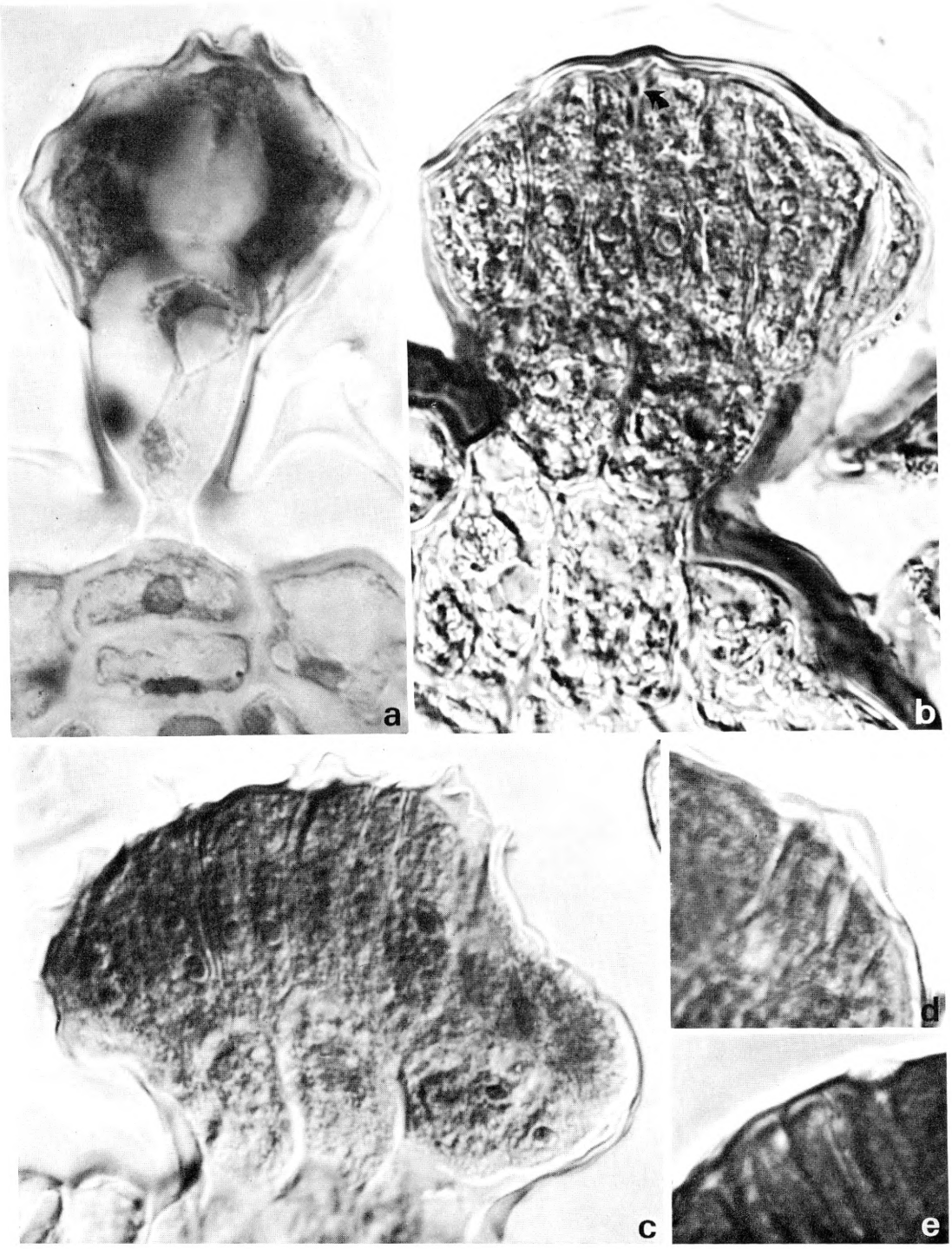
a
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Plate XXII

Neosparton ephedroides. a–c. SEM micrographs of surface. In (a) four furrows (× 50), in (b) and (c) one furrow (× 500 and ×1000). — d. Cross section of furrow (Safranin-Fast green, × 500).

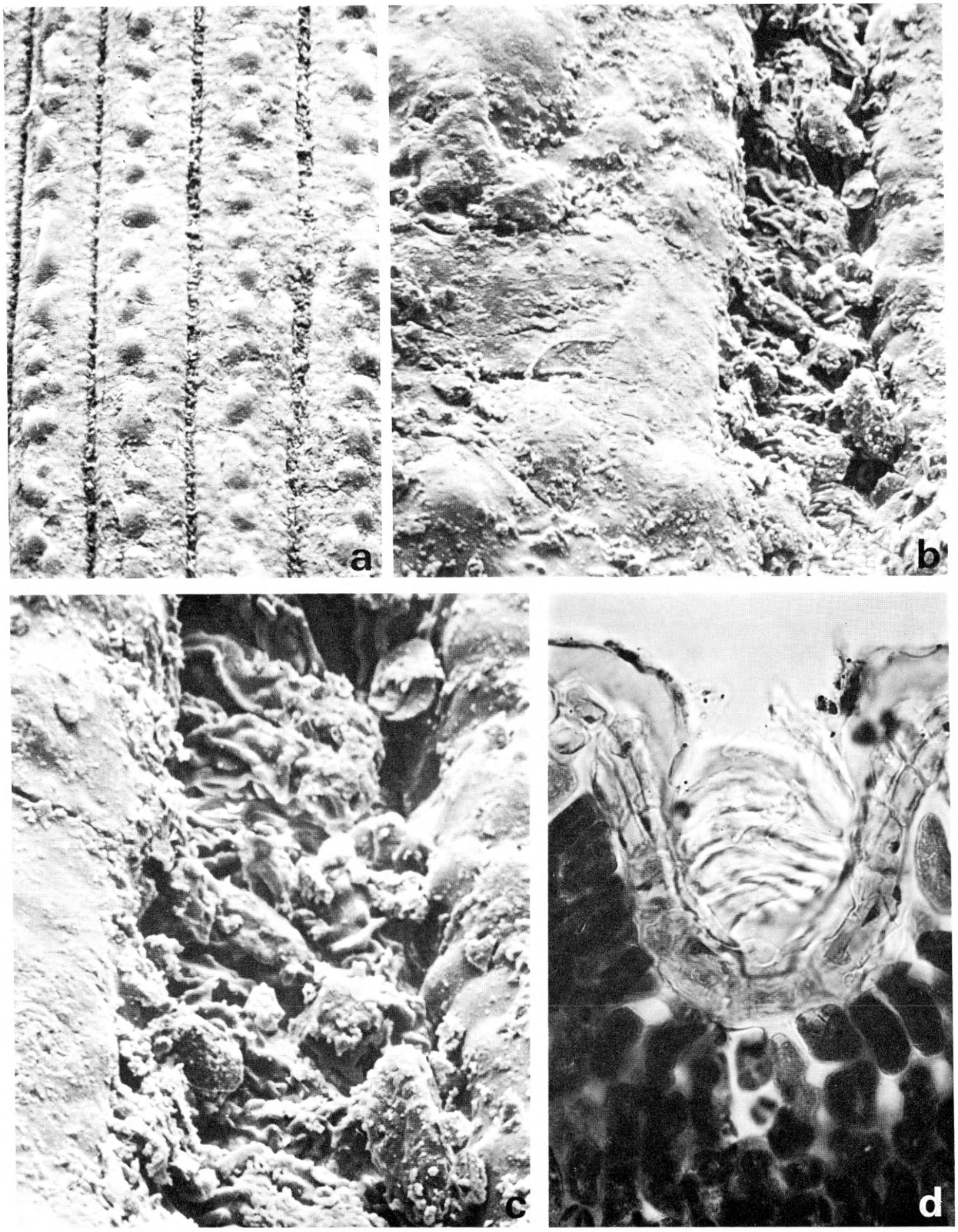
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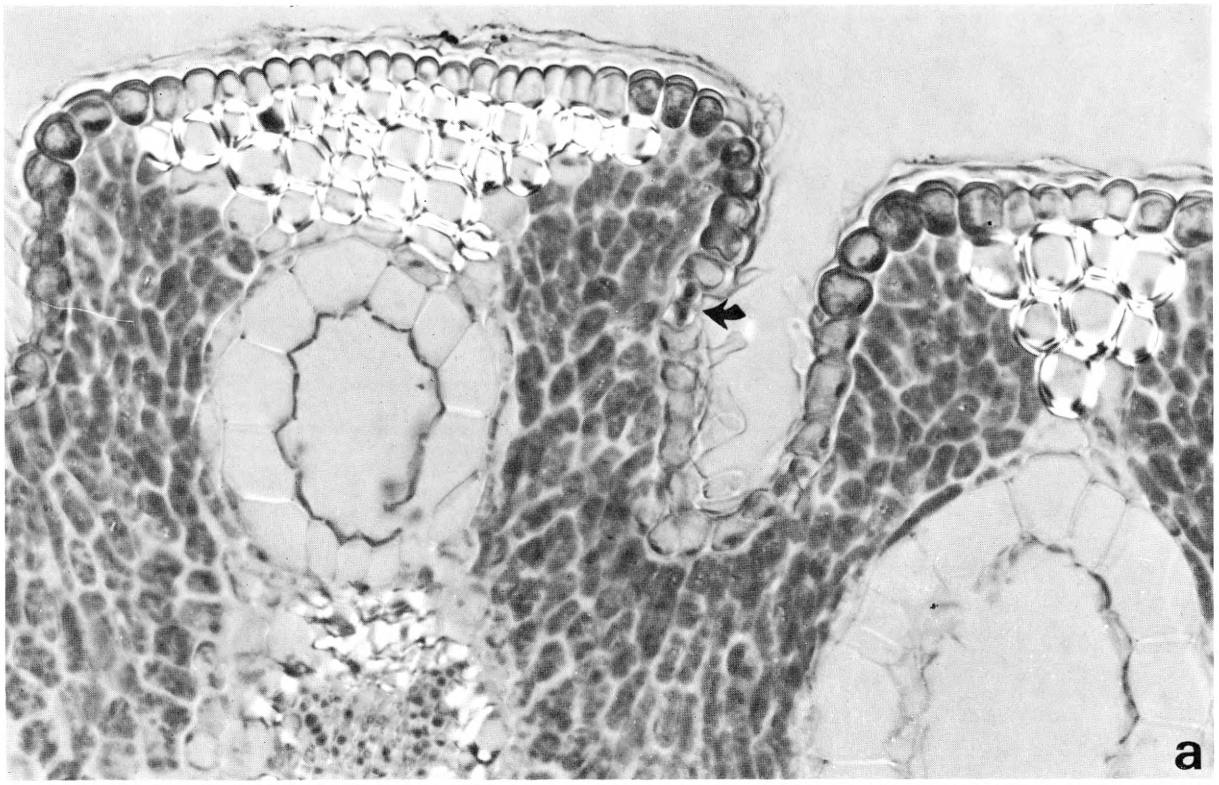
Plate XXIII

Aphyllocladus spartioides. a. Cross section of two ribs, a stomatal pore at the arrow. Sclerenchyma outside ducts. Peeling off of outer cuticular layer on top of ridges (Safranin-Fast green, polarized light, × 320). — b–c. SEM micrographs of surface, in (b) three furrows (× 100), in (c) one furrow with curled hairs and, on the right, a circular scar from hair which is shed while the cuticular layer has increased in thickness in its surroundings, cp. text p. 117 (× 1000).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