

COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENiaceae, V. LEAF ANATOMY*

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IN THE PRECEDING PAPER in this series (Dickison, 1969) I discussed the significance of nodal and leaf vascularization. The present article represents an extension of that study surveying additional features of leaf anatomy. It is hoped that the new information presented will help clarify the taxonomy, evolution, and generic definitions in this tropical family. All specimens studied have been cited with their respective collection data in my last paper. Though the lack of a complete collection of liquid-preserved specimens often prevented comparative observations, several new anatomical features are reported for the first time in the family.

Continued examination of leaf vascularization in the family has revealed a truly impressive range of variation, particularly in *Hibbertia*. In addition to differences in vein diameter and presence or absence of sheathing sclerenchyma pointed out earlier, the pattern and orientation of the veins is often diagnostic. For example, *H. glaberrima* can be distinguished by the orientation of veins at right angles to the long axis of the leaf (FIGURE 46), whereas *H. tomentosa* is characterized by a closed venation pattern, i.e., very few free vein endings. A careful investigation of this variation using a wide range of material might prove to be of unusual taxonomic importance. I have already drawn attention to the characteristic leaf venation of many needle-leaved hibbertias, viz., a prominent midvein with recurved laterals. The massive nature, in some species, of recurved secondary veins, as they terminate at the leaf base is illustrated by FIGURES 31 and 33. The extensive development of tracheary elements in this region of the leaf is not only of anatomical interest, but raises questions about possible physiological factors involved.

FOLIAR IDIOBLASTS

Foster (1956), in his review of plant idioblasts, recognizes three major categories of idioblastic cells — excretory, tracheoid, and sclerenchymatous. Examples of each class are found in leaves of the Dilleniaceae.

Excretory idioblasts. A common component of this heterogeneous assemblage are crystalliferous idioblasts. The occurrence of enlarged, raphide-containing cells is frequently cited as a primary character distinguishing the Dilleniaceae from other putatively related families (e.g., Cronquist, 1968). Since the distribution of raphides is limited in dicotyle-

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dons, their presence assumes greater taxonomic importance than other more common crystal types (Metcalf & Chalk, 1950). Gibbs (1958) is of the opinion that the presence of raphides is a primitive feature.

Raphides have been observed in the leaves of all dilleniaceous genera except *Schumacheria*. Crystals were found with equal frequency in both the petiole and lamina; however, within the lamina, there is a tendency for raphides to be restricted to either the spongy or palisade mesophyll. Those found in the palisade layers are usually orientated in an upright manner (FIGURE 27). The needle-like raphides are often produced in enlarged, thin-walled idioblasts containing an abundance of mucilage (FIGURES 5, 21, 27). Calcium oxalate is deposited early in ontogeny as shown by the occurrence of crystals in the hypocotyl and cotyledons of *Dillenia*, *Hibbertia*, and *Tetracera* (FIGURE 20).

Crystals intermediate in shape between raphides and crystal sand are prevalent in some members of the family, e.g., *Curatella*. Examples of this condition may be seen in the enlarged pith parenchyma cells of the midrib in *Doliocarpus olivaceus* (FIGURE 22). The "crystal complement" of the family also includes cuboidal and nearly prismatic crystals as observed in the petiole of *Doliocarpus guianensis* (FIGURE 56) and *Hibbertia pancheri*. The latter types have not previously been reported.

The distribution of crystalliferous cells in the phloem parenchyma of the petiole and midrib was noted by Metcalfe and Chalk (1950) in *Hibbertia scandens* (FIGURE 23). This condition seems to be characteristic of the family as a whole, having now been observed in *Curatella*, *Didesmandra*, *Dillenia*, *Doliocarpus*, and *Tetracera*.

The presence of silica containing cells in the Dilleniaceae has been known for some time. Workers have noted silicified cells in *Curatella*, *Davilla*, *Doliocarpus*, *Hibbertia*, and *Tetracera*. Silica deposition occurs throughout the parenchymatous regions of the leaf mesophyll and epidermis as either fine granular particles within the cell lumen (FIGURE 54), or larger bodies impregnating the cell wall and intercellular cavities (FIGURE 55). The abundance of these silica deposits, combined with crystals and sclerified trichomes, makes it possible to use the leaves of *Curatella*, *Davilla*, and *Tetracera* as sandpaper (Standley & Williams, 1961).

Representing a third type of excretory idioblast of Dilleniaceae are the widely distributed "mucilaginous cells" (FIGURE 57). It is of particular interest that Parmentier (1896) referred to the presence of "cellules oléigènes" in the mesophyll of *Hibbertia scabra* and suggested their occurrence was an excellent character to show the affinities of the Dilleniaceae to the Magnoliaceae. Although the chemical nature of the cell mucilage is unknown, these idioblasts do not appear comparable to the "ethereal oil cells" of many ranalian families. The large oil sac or drop, as well as scent, described by Wilson (1965) as being characteristic of ranalian oil cells is lacking. Structurally, the enlarged mucilage cells differ considerably in size and form. Intergradations with raphide-containing idioblasts are common.

Tracheoid idioblasts. Cleared leaves of *Hibbertia montana* (E. H.

Wilson 476), *H. vestita* (NSW 55998), and *H. subvaginata* (C. L. Wilson 764) revealed idioblasts which closely resemble the tracheoid type (FIGURE 47). The cells in question resemble typical tracheids in their spirally-thickened walls, general size and form, but are found completely isolated from other venation. They never occur in abundance. No evidence of undifferentiated procambium is present between these cells and the leaf vein. It is assumed, accordingly, that they arise in the lamina from the ground meristem. The best classification of these cells would probably be "storage tracheids" although there is no evidence to support their water-storing capacity.

The occurrence of elements of this sort in *Hibbertia* is of particular interest. Emphasis has already been put on the highly diverse vein endings in many species of this genus and a varied foliar sclereid composition will be described subsequently. It is evident, therefore, that within this single taxon is present a wide diversification of idioblast morphology. Foster (1956) pointed out that the morphological relationship between the various foliar idioblasts represents a complex problem which merits further careful study. I would suggest that *Hibbertia* represents extremely favorable material for such an investigation.

Sclerenchymatous idioblasts. Sclerenchymatous vein sheathing is present in the leaves of many Dilleniaceae (Dickison, 1969). This sclerenchyma, which often becomes massive (FIGURE 32), and encloses the terminal tracheids, is encountered in the petiole in the form of perivascular fibers (see Esau, 1965, p. 209) either capping vascular bundles or forming a continuous cylinder. In the larger veins of the lamina, sheathing extends from the adaxial to the abaxial surface.

The first report of sclereids in leaves of Dilleniaceae was by Steppuhn (1895) who described the occurrence of thick-walled, branched "spicular" cells in two species of *Hibbertia*. Further comprehensive examination, however, has revealed a much wider range of foliar sclereid morphology and distribution. Although sclereids are wide-spread in the family, they reach greatest diversity in *Hibbertia*. On the basis of their distribution, it is convenient to distinguish four types: (1) sclereids diffuse in the mesophyll (and pith and cortex of petiole), (2) sclereids terminal at vein endings, (3) epidermal sclereids, and (4) sclereids subtending trichomes.

With regard to the first category, various forms of sclereids are present: clusters of unbranched brachysclereids ("stone cells") are occasionally found in large numbers in the cortex and pith in petioles of *Davilla*, *Doliocarpus* (FIGURE 56), *Hibbertia* and *Schumacheria*; FIGURE 9 shows an abundance of these sclereids in the leaf base of *Hibbertia altigena*; in addition to the elongate sheathing fibers, the midvein of several species may also be enclosed by short, unbranched sclereids. In one collection of *Doliocarpus major* (von Wedel 2860) such sclereids are located along the periphery of the lamina (FIGURE 7). The conspicuous sclereids in *Hibbertia lucida* (FIGURE 3), *H. oubatchensis* (FIGURE 2), *H. pancheri*, and *H. patula* (FIGURE 1) all tend to be irregularly branched. These "armed," thick-walled sclereids occur in clusters throughout the mesophyll and

parenchymatous regions of the petiole. Very distinctive osteosclereids are present in the lamina of *H. salicifolia* (FIGURE 4). The latter cells, for the most part, are oriented with their long axis parallel to the long axis of the leaf. A fourth form of diffuse idioblast is the truly stellate sclereid (astrosclereids) found in the lamina of *H. crenata* (FIGURE 13).

In contrast to the above conditions, sclereids in *Hibbertia lasiopus*, *H. miniata*, *H. montana*, *H. obtusifolia*, and *H. saligna* are prevailing associated with terminal veinlets. In the leaves of *H. lasiopus* (C. L. Wilson 781), *H. miniata* (C. L. Wilson 782), *H. montana* (C. L. Wilson 838), and *H. obtusifolia* (Pullen 3882) the idioblasts are parenchymatous, mostly unbranched, or provided with only rudimentary branches, and occur in clusters at, or in the vicinity of, the terminal tracheids (FIGURE 10). Along the margin of the lamina, however, are located extensively branched, stellate sclereids (FIGURE 11).

The terminal idioblasts of *Hibbertia saligna* (Constable 43107), on the other hand, are highly branched and occur singly at virtually all vein endings (FIGURE 12). In his paper on the terminal sclereids in *Mouriria*, Foster (1946) describes terminal cells intermediate in character between normal tracheary elements and sclereids. I have observed similar "transitional cells" in *Hibbertia*, again indicating the possible ontogenetic relationship between terminal sclereids and terminal tracheary elements. When the various terminal idioblastic cells described in my previous paper (Dickison, 1969) are considered in conjunction with the terminal sclereids now reported, the tremendous diversity of vein endings in this genus becomes evident.

Next to be considered is epidermal sclerification, which, once again, is present in *Hibbertia*. Of particular note are the massive, thick-walled cells in the upper epidermis of *H. nana*. The striking nature of these isolated sclereids may be seen in surface view in FIGURE 8. In sectioning, these cells are usually torn free leaving behind large spaces in the hypodermis (FIGURE 26). In many of the needle-leaved hibbertias, the entire epidermis becomes sclerified. Depending upon the species, the epidermal cells have wavy anticlinal walls (e.g., *H. mucronata*, FIGURE 6), or straight walls with overlapping ends (e.g., *H. acicularis*, FIGURE 48). Sclerification of the epidermis in these species appears to be a specialization related to the xerophytic habit. Another unique feature observed only in *Dillenia ochreatea* was the intensive sclereid development in the petiole wings (FIGURE 5).

The last diagnostic sclereids in the leaves of Dilleniaceae are those which subtend the spiny, sclerified trichomes in *Tetracera*. This condition, which was first reported by Solereder (1908), has been observed only in the African species *T. leiocarpha*, the New World species *T. ovalifolia* and *T. portobellensis*, and an unnamed Krukoff collection from Brazil (Krukoff 6430). As seen in FIGURES 14, 15, and 17, these columnar cells traverse the mesophyll immediately under the compound trichomes. Usually only a single sclereid is present under each trichome fascicle, but in the Krukoff collection a large cluster of sclereids is present. Although these sclereids

are typically unbranched, they may become branched to varying degrees (FIGURE 16). The relationship between trichomes and sclereid formation in these plants is not clear. Their limited distribution, however, suggests they are of good systematic value. Moreover, the entire range of sclereid morphology in the family appears to be of potential taxonomic importance.

TRICHOMES

The scabrous nature of dilleniaceous leaves is well known to those familiar with the family. Solereder (1908) and Metcalfe and Chalk (1950) describe the trichome composition as consisting of simple unicellular, stellate, and rarely peltate hairs. The complete trichome complement of the family, however, has never been adequately illustrated.

Simple unicellular trichomes are the most common form in the family, being present in all genera. Significant fluctuations are found in the length, form, and distribution of these hairs. Gradations in length occur from the narrow, very elongate (up to 1600μ) trichomes in species of *Acrotrema* (FIGURE 41), *Didesmandra* and *Dillenia*, to the very short, pointed type seen in *Doliocarpus* (FIGURE 44). These hairs may be thick-walled, straight and highly sclerified (FIGURES 13, 26), or, thin-walled and curled (FIGURES 19, 59). Distinctive short, thick-walled, curved hairs are present on the lower epidermis of *Hibbertia baudouinii* (FIGURE 28). Simple unicellular trichomes also may become silicified (e.g., *Davilla*).

Stellate trichomes are present in *Curatella* (FIGURE 45) and *Hibbertia* (FIGURES 30, 34). Various forms of fasciculate trichomes with unicellular rays are common in the family. In *Curatella* (FIGURE 45), *Didesmandra* (FIGURE 43), and *Tetracera* (FIGURES 14, 15) the rays are reduced to spines. Gradation between spiny fascicles and the stellate condition can be seen in FIGURES 17 and 58. The walls of these cells are sclerified and/or incrustated with silica. Although peltate hairs have been reported for *Hibbertia lepidota*, I have not observed true peltate trichomes during this study. I do not believe, furthermore, that the drawing by Solereder (*loc. cit.*, p. 22) represents a truly peltate condition but rather an asteroid modification of the fasciculate type.

A short, highly silicified, blunt-tipped, papillate trichome is prevalent in many species of *Dillenia* (FIGURES 40, 60, 61). In surface view these trichomes are irregular in outline (FIGURE 61). In some species this may be the only type of trichome present. In species which possess both unicellular and papillate trichomes, their distribution seems to be of diagnostic value (see FIGURES 60, 61).

Although the Dilleniaceae have long been thought to lack glandular trichomes, I am now reporting this feature for the first time in the family. Trichomes with typical glandular morphology, i.e., stalk and multicellular head, were found in *Dillenia philippinensis* and *D. reifferscheidia*. FIGURE 39 shows their location in depressions on the abaxial surface of the lamina.

EPIDERMIS AND STOMATA

Following the early work of Parmentier (1896), the Dilleniaceae have been regarded by subsequent investigators (e.g., Solereder, 1908, and Metcalfe & Chalk, 1950) as possessing stomata of the ranunculaceous (anomocytic) and rubiaceous (paracytic) types. A lack of adequate liquid-preserved specimens has prevented critical observations on the epidermis of *Acrotrema*, *Doliocarpus*, and *Schumacheria*; nevertheless, my preliminary studies reveal a wider range of structural variation than previously suspected. Although the systematic significance of this variation cannot be assessed at present, the type of stomatal apparatus, size of guard cells, size and undulation of ordinary epidermal cells, and presence of cuticular striations appear to be of potential taxonomic value.

Stomata are confined without exception to the abaxial leaf surface (FIGURE 27). In many hibbertias they are located in stomatal crypts or grooves. Stomatal crypts are prevalent among many New Caledonian species, e.g., *H. baudouinii* (FIGURE 28), *H. nana* (FIGURE 26), *H. pancheri* (FIGURE 25), *H. pulchella*, *H. tontoutensia*, *H. trachyphylla*, and *H. wagapii*. Stomatal grooves extending the length of the lamina are characteristic of most xerophytic, needle-leaved Australian species. Differences occur in the shape of the groove and in the trichome distribution. *Hibbertia pungens* (FIGURE 35) illustrates a condition where hairs completely fill the groove. In *H. uncinata* (FIGURE 37) trichomes are located only at the opening whereas in *H. pachyrhiza* (FIGURE 36) the grooves lack trichomes. FIGURE 36 also shows the thick cuticle formation in many of these species along with prominent striations.

The leaves of *H. gilgiana* are distinguished by the anticlinal walls of both upper and lower epidermal cells being arched at the point of contact (FIGURE 29). It can also be seen that the stomata are noticeably raised. A conspicuously papillate epidermis is also present in many species (e.g., *H. baudouinii*, FIGURE 28).

Reference has previously been made to elongate, sclerified epidermal cells in xerophytic hibbertias (FIGURE 48). The outer wall of these cells is frequently thickened and provided with papillae. Epidermal cells surrounding the spiny, fasciculate trichomes become differentiated by their thickened walls and lack of undulation. The epidermal cells of *Doliocarpus olivaceus* appear very distinctive in being circular and highly undulate. Unfortunately I did not have good material for study of this species. Silicification of the epidermis has been noted in *Curatella* (FIGURE 45), *Davilla*, *Didesmandra*, *Dillenia*, *Hibbertia*, and *Tetracera*.

With regard to stomatal apparatus, *Tetracera* and *Didesmandra* possess the rubiaceous type. The two parallel subsidiary cells are distinguishable from the surrounding epidermal cells by their shape and dark contents (FIGURE 50). Guard cells vary in length from 20 to 35 μ . The epidermis of *Didesmandra* is perhaps the most distinctive in the family. The anticlinal walls of epidermal cells are undulate, guard cells lack chloroplasts, and

cuticular striations are orientated at right angles to the obliquely orientated subsidiary cells (FIGURE 49).

The stomatal structure in *Curatella*, *Davilla*, *Dillenia*, and *Hibbertia* is predominantly ranunculaceous, since no subsidiary cells are evident (FIGURE 53). Considerable variation does occur, however, in the undulation of epidermal cells and size of guard cells. Within the family guard cells range in length from 16 to 36 μ . Uniformly small guard cells (under 20 μ) were found in *Curatella*, *Davilla*, *Dillenia ovata*, and *Doliocarpus major*.

Of particular interest is the stomatal apparatus encountered in *Hibbertia tetrandra*. A careful examination showed it to be unlike all other Dilleniaceae examined, as it could properly be classified as "gordoniaceous" (FIGURE 51). The gordoniaceous stomatal apparatus (*sensu* Keng, 1962) is described as consisting of guard cells surrounded by two to four subsidiary cells which differ from ordinary epidermal cells in narrower cell shape and in their reaction to chemical reagents. In *Hibbertia* the number of subsidiary cells varies from four to six. Keng (*loc. cit.*) tentatively named this stomatal apparatus for the theaceous genus *Gordonia* in which it was first described by Solereder (1908), who has subsequently considered it as characterizing the subfamily Camellioideae of the Theaceae.

In view of the apparent restricted distribution of the gordoniaceous type of stomatal apparatus, its presence in the Dilleniaceae seems to be of special significance in relating these two families.

MESOPHYLL

The mesophyll of dilleniaceous leaves displays considerable differentiation at both generic and specific levels. Each genus has a distinctive combination of characters. In addition to the specialized idioblasts already mentioned, anatomical features of the mesophyll which demonstrate variation are: thickness, presence or absence of a hypodermis and its location on the adaxial or abaxial surface, bifacial or isolateral nature, number of palisade layers, and presence or absence of intercellular spaces in the spongy layers. A comparison of these features in all genera excluding *Hibbertia* is listed in TABLE 1. It should be noted that a hypodermis is found in some species of *Dillenia*. Also, the correlation between the coriaceous texture of the leaf, its multiple palisade layers, and a complex petiolar anatomy is noteworthy in *Doliocarpus*.

The largest number of anatomical specializations, however, is found in the leaves of *Hibbertia* where extreme adaptations to environment have occurred. A few selected species listed in TABLE 2 exemplify the range of diversification.

DISCUSSION

In response to extremes in the habitat, the leaves of Dilleniaceae exhibit marked differences in form, texture and thickness. Correlated with external

TABLE 1. Anatomical Comparison of Leaf Mesophyll in Dilleniaceae
(excluding *Hibbertia*).

TAXON	NUMBER OF LAYERS IN ADAXIAL HYPODERMIS	NUMBER OF LAYERS IN ABAXIAL HYPODERMIS	NUMBER OF PALISADE LAYERS	INTER- CELLULAR SPACES
<i>Acrotrema</i> (adequate material not available for study)				
<i>Curatella</i> (FIG. 45)	—	—	2, ± isolateral	sparse
<i>Davilla</i>	—	—	2	sparse
<i>Didesmandra</i> (FIG. 43)	—	—	1	abundant
<i>Dillenia excelsa</i>	1	—	2-3	moderate
<i>D. indica</i>	—	—	2	moderate
<i>D. megalantha</i>	1-2	—	2	moderate
<i>D. ovata</i>	—	—	1	moderate
<i>D. papuana</i>	2	—	2-3	abundant
<i>D. philippinensis</i>	1	—	1	moderate
<i>D. pulchella</i> (FIG. 38)	2	1	2	moderate
<i>D. reifferscheidia</i> (FIG. 39)	1-2	1-2	2	moderate
<i>D. suffruticosa</i> (FIG. 40)	—	—	2-3	abundant
<i>Doliocarpus</i> sp. (Pires et al. 52254)	—	—	3	sparse
<i>D. calineoides</i> (FIG. 44)	—	—	2	moderate
<i>D. coriaceus</i>	—	—	2-3	sparse
<i>D. dentatus</i>	—	—	1	moderate
<i>D. guianensis</i>	—	—	2-3, ± isolateral	moderate
<i>D. lasiogyne</i>	—	—	1-2	sparse
<i>D. olivaceus</i> (FIG. 42)	—	—	1	abundant
<i>Schumacheria castaneifolia</i>	—	—	2-3	abundant
<i>Tetracera indica</i>	—	—	1	moderate
<i>T. scandens</i> (FIG. 18)	—	—	2-3	moderate

differences, are a number of highly divergent trends of anatomical specialization which parallel those that occur in the dicotyledons as a whole.

In arid environments, dilleniaceous leaves have become either increasingly coriaceous or reduced in size. Coriaceous leaves are generally distinguished by formation of multiple palisade layers, a tendency to become isolateral, an absence of intercellular spaces, sclerification of trichomes, intensive sclerification along the veins and veinlets, formation of sclereid clusters in the mesophyll, and in *Hibbertia*, development of abaxial stomatal crypts. In *H. patula* a tremendous increase in leaf thickness is the result of extensive development of spongy mesophyll.

In other hibbertias, in contrast, (e.g., *H. gilgiana*) the lamina has become reduced in thickness resulting in a poorly differentiated mesophyll.

Progressive reduction in leaf size in *Hibbertia* has proceeded along several distinct lines. The result of this specialization is the production of reduced leaves of very diverse form and shape. The ultimate reduction in leaf evolution has taken place in the genus *Pachynema* where only scale-like projections are present (although they are still morphologically megaphylls). Xerophytic modification is evident in the ericoid habit, the

TABLE 2. Anatomical Comparison of Leaf Mesophyll in *Hibbertia*

TAXON	HYPODERMIS (MULTIPLE EPIDERMIS?)	NUMBER OF LAYERS IN PALISADE	ABAXIAL PALISADE	ABAXIAL CRYPTS OR GROOVES	INTER- CELLULAR SPACES	LEAF FORM AND TEXTURE
<i>H. cuneiformis</i> (FIG. 27)	—	1	—	—	moderate	flat
<i>H. baudouinii</i> (FIG. 28)	—	2	—	crypts	sparse	flat
<i>H. gilgiana</i> (FIG. 29)	mesophyll not clearly differentiated			—	moderate	flat-thin
<i>H. nana</i> (FIG. 26)	1 layered	1	+	crypts	sparse	flat- coriaceous
<i>H. pancheri</i> (FIG. 25)	—	2-3 (4)	—	crypts	moderate	flat
<i>H. patula</i> (FIG. 24)	—	1-2 (extensive spongy mesophyll)	—	sunken stoma	abundant	flat-thick
<i>H. pungens</i> (FIG. 35)	—	1	+	grooves	moderate	ericoid
<i>H. sericea</i> (FIG. 30)	—	1	—	—	moderate	inrolled margins
<i>H. teretifolia</i>	—	1	+	—	sparse	terete

lamina with inrolled margins, and in *H. teretifolia*, a terete leaf form. Such specializations are often associated with intensification of vascularization and reflexed venation, sclerification of trichomes and epidermal cells, formation of abaxial palisade, and absence of intercellular spaces. It is interesting to note that the needle-leaved hibbertias generally do not exhibit sclerified vein sheathing.

In both the broad-leaved and needle-leaved species of *Hibbertia*, there has also occurred a wide range of morphological diversification of the terminal tracheary elements. It is evident, accordingly, that the anatomy of the dilleniaceous leaf, in many instances, has become highly specialized and directly reflects the modifying influence of environmental extremes.

Carlquist (1961) indicated that the leaf is perhaps anatomically the most varied organ of angiosperms, and as a result often contains numerous characters of taxonomic importance. Leaf anatomy of the Dilleniaceae has been shown to possess a considerable amount of variation which heretofore has not been fully exploited for systematic purposes. When the nodal and petiolar anatomy is considered in conjunction with characters from the lamina, the dilleniaceous genera are sharply defined. In many instances, excellent specific characters have been pointed out as well.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1-4. Foliar sclereids. FIG. 1, *Hibbertia patula* (McKee 3543), sclereids photographed in polarized light between crossed nicols, $\times 51$. FIG. 2, *H. oubatchensis* (McKee 3306A), $\times 132$. FIG. 3, *H. lucida* (C. T. White 2210), $\times 208$. FIG. 4, *H. salicifolia* (C. L. Wilson 625), cleared leaf showing elongate osteosclereids oriented parallel to long axis of leaf, $\times 51$.

PLATE II

FIGS. 5-9. Foliar sclereids. FIG. 5, *Dillenia ochreatea* (NIFS bb18085), cleared petiole wing showing extensive sclereid development, $\times 52$. FIG. 6, *Hibbertia mucronata* (C. L. Wilson 792), cleared leaf showing epidermal sclereids with undulating anticlinal walls, $\times 52$. FIG. 7, *Doliocarpus major* (von Wedel 2860), cleared leaf showing unbranched sclereids along margin of lamina, $\times 132$. FIG. 8, *Hibbertia nana* (Baumann-Bodenheim 15358), cleared leaf showing massive epidermal sclereids, $\times 52$. FIG. 9, *H. altigena* (McKee 3709), base of leaf containing numerous unbranched sclereids, $\times 52$.

PLATE III

FIGS. 10-13. Foliar sclereids. FIG. 10, *Hibbertia lasiopus* (C. L. Wilson 781), note sclereids tend to be situated at vein endings, $\times 52$. FIG. 11, *H. montana* (C. L. Wilson 838), cleared leaf photographed in polarized light between crossed nicols. Note extensively branched sclereids along periphery of lamina, $\times 52$. FIG. 12, *H. saligna* (Constable 43107), cleared leaf showing branched, terminal sclereids, $\times 133$. FIG. 13, *H. crenata* (C. L. Wilson 851), transverse section of lamina showing stellate sclereids in mesophyll and sharply pointed, sclerified trichomes, $\times 209$.

PLATE IV

FIGS. 14-19. Leaf anatomy of *Tetracera*. FIG. 14, *T. ovalifolia* (Johnston 1140), cleared leaf showing compound, sclerified trichomes with subtending sclereids (arrows), $\times 52$. FIG. 15, *the same*, transverse section of lamina, $\times 208$. FIG. 16, *T. leiocarpa* (Cooper 45), isolated branched sclereid illustrating thick, pitted wall, $\times 520$. FIG. 17, *T. portobellensis* (Steinbach 7229), transverse section of lamina showing sclerified, fasciculate trichomes with subtending sclereids, $\times 208$. FIG. 18, *T. scandens* (M. Q. Lagrimas s.n., Makiling, Philippines), transverse section of leaf, $\times 208$. FIG. 19, *T. boiviniana* (Tanner 2548), transverse section of lamina showing undulating abaxial surface and curled trichomes, $\times 208$.

PLATE V

FIGS. 20-23. Varied forms of crystals in leaves. FIG. 20, *Tetracera indica* (seedling grown from seed supplied by H. Keng), cleared cotyledon showing numerous raphides, $\times 54$. FIG. 21, *T. akara* (Elmer 21314), cleared leaf showing raphide-containing idioblast. Also note the much branched mesophyll parenchyma, $\times 210$. FIG. 22, *Doliocarpus olivaceus* (Stern et al. 11), transverse section of midrib showing enlarged, crystal containing pith cells. The crystals are transitional between raphides and crystal sand. Also note the complete vascular cylinder and the lack of medullary bundles, $\times 135$. FIG. 23, *Hibbertia scandens* (Cult. E C4386), transverse section of midrib illustrating enlarged crystal-containing phloem parenchyma cells, $\times 210$.

PLATE VI

FIGS. 24-30. Leaf anatomy of *Hibbertia*. FIG. 24, *H. patula* (McKee 3543), transverse section showing extensive mesophyll development, sunken stomata (st), foliar sclereids, and sclerenchyma surrounding vein, $\times 54$. FIG. 25, *H. pancheri* (Thorne 28585), transverse section showing multilayered palisade mesophyll and stomatal crypts, $\times 54$. FIG. 26, *H. nana* (Baumann-Bodenheim 15358), transverse section showing hypodermis with epidermal sclereid torn free, isolateral mesophyll, stomatal crypt, and sclerified trichomes on lower surface, $\times 54$. FIG. 27, *H. cuneiformis* (Cult. K s.n.), transverse section illustrating single layered palisade with raphide idioblast and stomata (st) on lower surface, $\times 132$. FIG. 28, *H. baudouinii* (Baumann-Bodenheim 11203), transverse section showing lack of intercellular spaces in mesophyll, papillate lower epidermis, and short, curved trichomes (tr), $\times 52$. FIG. 29, *H. gilgiana* (C. L. Wilson 856), transverse section of lamina illustrating weakly differentiated mesophyll, arching epidermal cells and raised guard cells (st), $\times 135$. FIG. 30, *H. sericea* (Muir 855), transverse section showing stellate, sclerified trichomes, $\times 52$.

PLATE VII

FIGS. 31-37. Leaf anatomy of *Hibbertia* [continued]. FIG. 31, *H. uncinata* (E. H. Wilson 155), basal portion of cleared leaf showing massive formation of tracheary elements in the recurved secondary veins, $\times 52$. FIG. 32, *H. australis* (Aston 359), transverse section of midrib showing well-developed fibers on abaxial side, $\times 140$. FIG. 33, *H. cistifolia* (Specht 843), transverse section of base of leaf illustrating prominent central midrib and extensive tracheary tissue on either side. Note absence of sheathing sclerenchyma, $\times 53$. FIG. 34, *H. tomentosa* (Specht 638), surface view of stellate trichomes, $\times 135$. FIG. 35, *H. pungens* (Royce 7640), transverse section of leaf showing ericoid habit. In this species trichomes completely fill the stomatal grooves. Also note adaxial and abaxial palisade layer, $\times 53$. FIG. 36, *H. pachyrhiza* (C. L. Wilson 861), transverse section of stomatal groove showing absence of trichomes and wavy cuticle, $\times 210$. FIG. 37, *H. uncinata* (E. H. Wilson 155), transverse section of stomatal groove showing trichome formation only at entrance, $\times 210$.

PLATE VIII

FIGS. 38-45. FIG. 38, *Dillenia pulchella* (Cult. SING s.n.), transverse section of lamina showing adaxial and abaxial hypodermis. Large spaces represent sites of crystal deposition, $\times 132$. FIG. 39, *D. reiffersheidia* (M. Q. Lagrimas s.n., Quezon, Philippines), transverse section of lamina illustrating sunken, glandular trichome on lower surface, $\times 132$. FIG. 40, *D. sufruticosa* (Cult. SING s.n.), transverse section of lamina showing silicified, papillate trichome (arrow) on lower surface, $\times 132$. FIG. 41, *Acrotrema* sp. (us 1576875), cleared leaf showing elongate, unbranched trichomes distributed along the major veins, $\times 22$. FIG. 42, *Doliocarpus olivaceus* (Stern et al. 11), transverse section of lamina, $\times 135$. FIG. 43, *Didesmandra aspera* (from Sarawak, s.n.), transverse section showing thin mesophyll and sclerified trichome, $\times 135$. FIG. 44, *Doliocarpus calineoides* (G. T. Prance et al. 3830), transverse section showing two-layered palisade and short, spiny trichomes (tr) on lower surface. Separation of tissue is the result of preparation, $\times 135$. FIG. 45, *Curatella americana* (Irwin 5470), transverse section of lamina illustrating lack of intercellular spaces, undulating abaxial surface, tendency toward isolateral mesophyll, silicification of epidermis, stellate and spiny trichomes, $\times 135$.

PLATE IX

FIGS. 46-48. FIG. 46, *Hibbertia glaberrima* (Perry 5379), cleared leaf showing tendency of veins to be orientated at right angles to long axis of lamina, $\times 26$. FIG. 47, *H. subvaginata* (C. L. Wilson 764), cleared leaf showing isolated tracheary idioblast, $\times 160$. FIG. 48, *H. acicularis* (Clemens 43622), cleared leaf showing elongate epidermal sclerenchyma, $\times 160$.

PLATE X

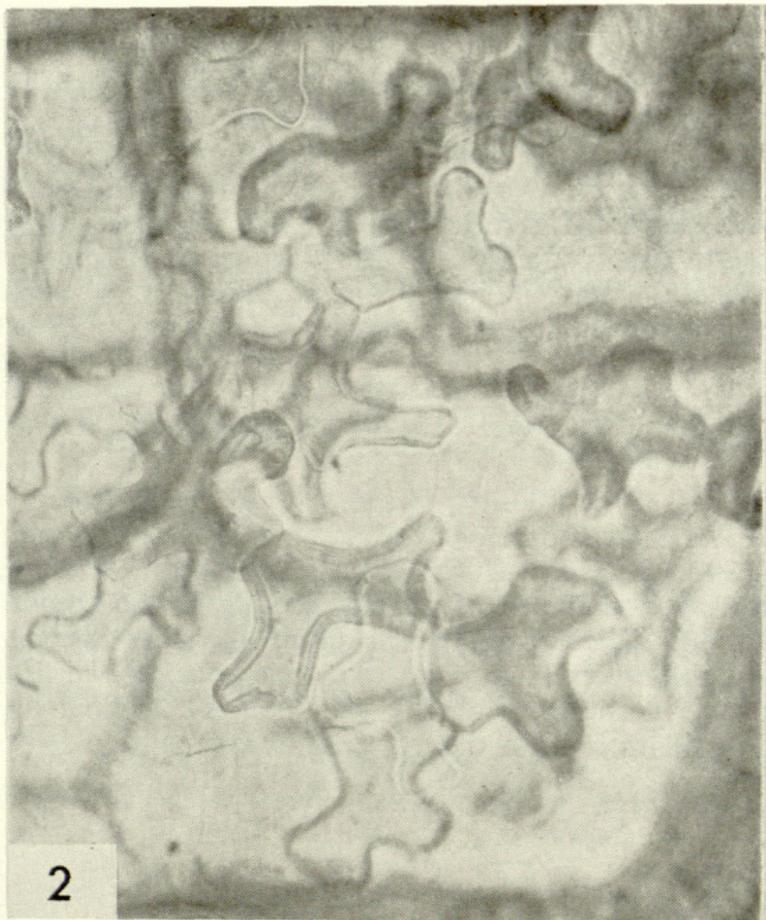
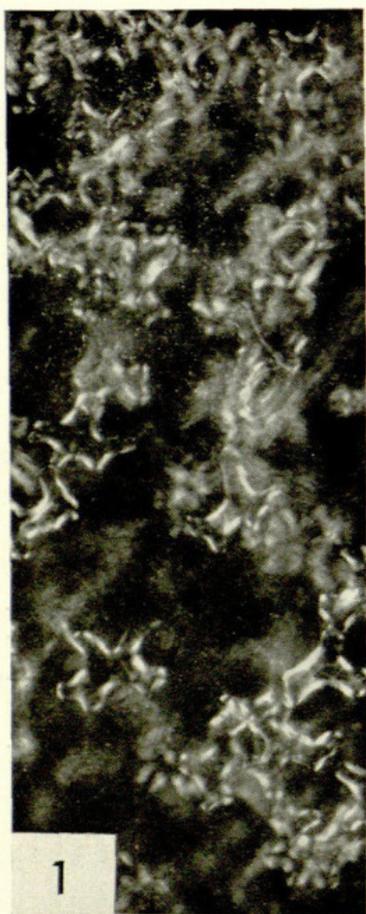
FIGS. 49-53. Lower epidermal layers of leaves preserved in FAA and mounted unstained. FIG. 49, *Didesmandra aspera* (from Sarawak, s.n.), note undulating anticlinal walls of epidermal cells, cuticular striations, and absence of chloroplasts in guard cells, $\times 163$. FIG. 50, *Tetracera indica* (H. Keng, s.n., from Singapore), note two parallel subsidiary cells (sc), $\times 163$. FIG. 51, *Hibbertia tetrandra* (Cult. E C3544), "gordoniaceous" stomatal apparatus with five subsidiary cells (sc), $\times 650$. FIG. 52, *H. dentata* (Cult. K s.n.), note undulating anticlinal walls of epidermal cells, prismatic bodies (arrow), and striations around stomatal apparatus, $\times 163$. FIG. 53, *H. scandens* (Cult. K s.n.), note the epidermal cells are not wavy although they do possess primary pit fields. The stomatal apparatus is ranunculaceous, $\times 163$.

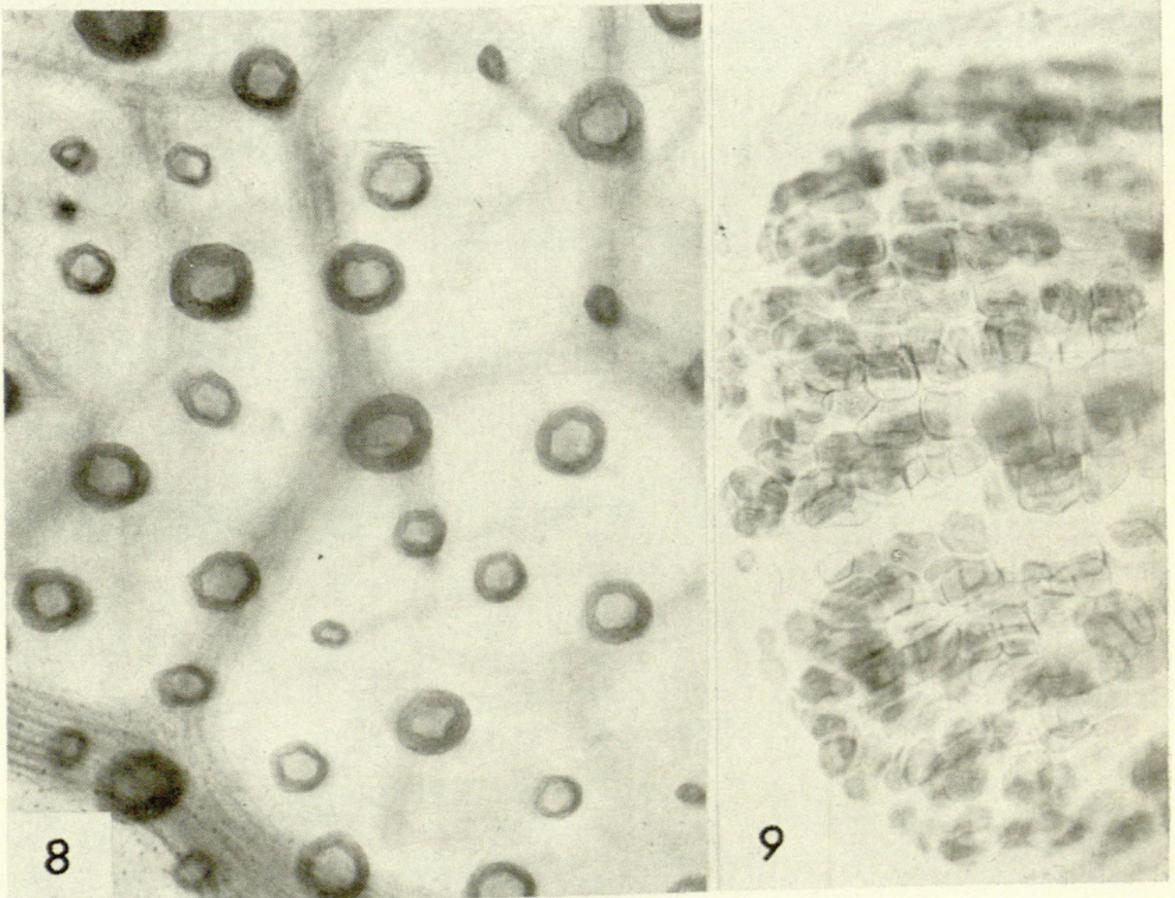
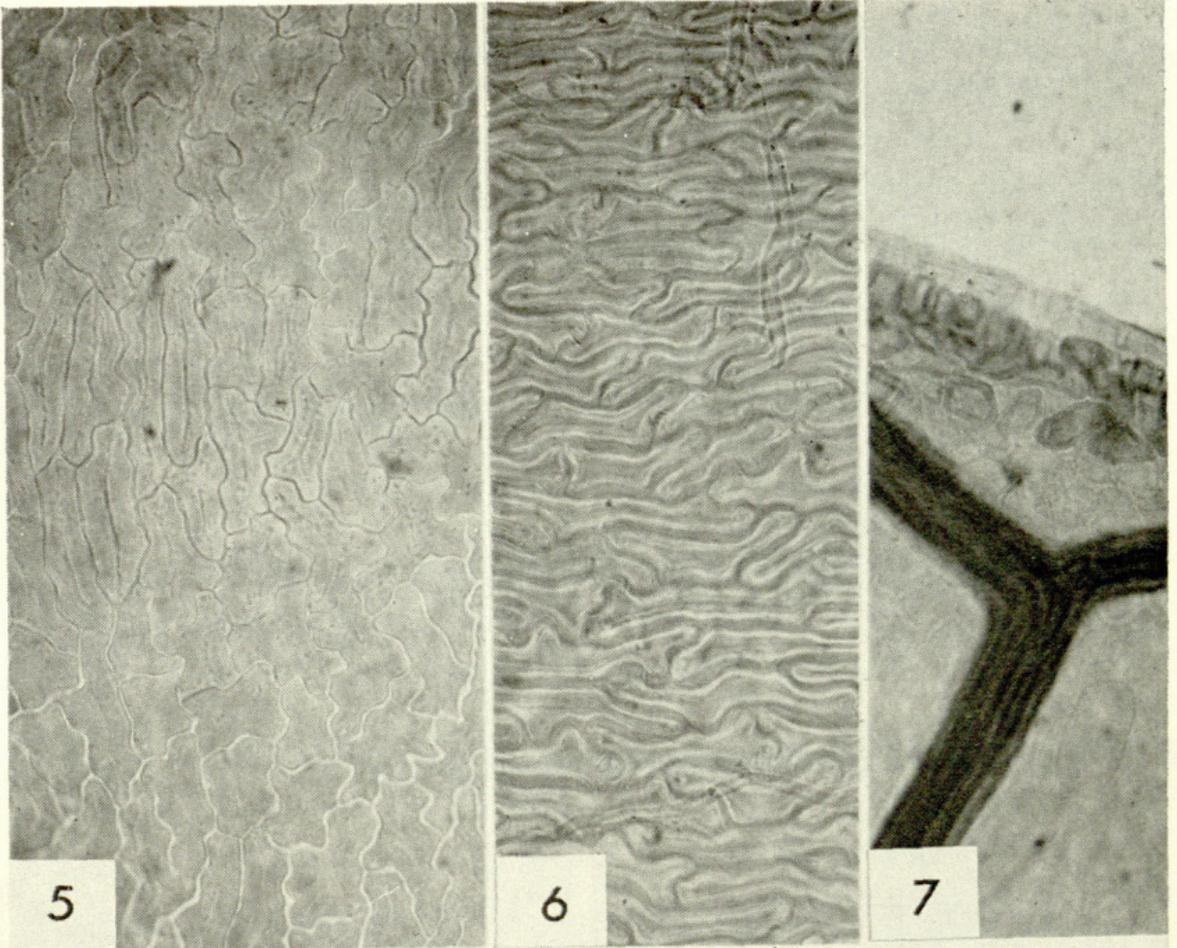
PLATE XI

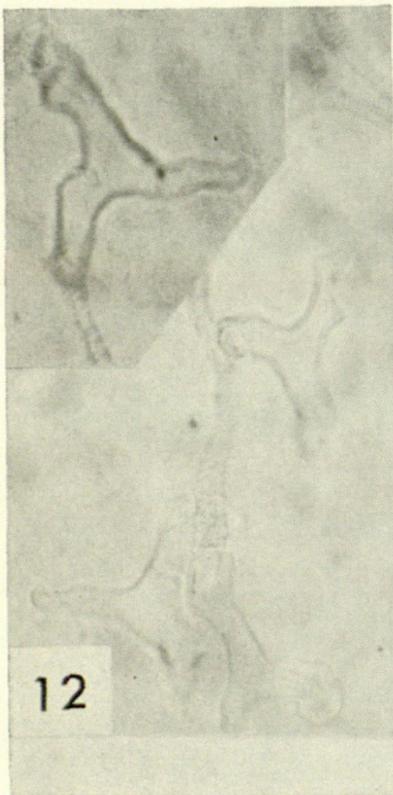
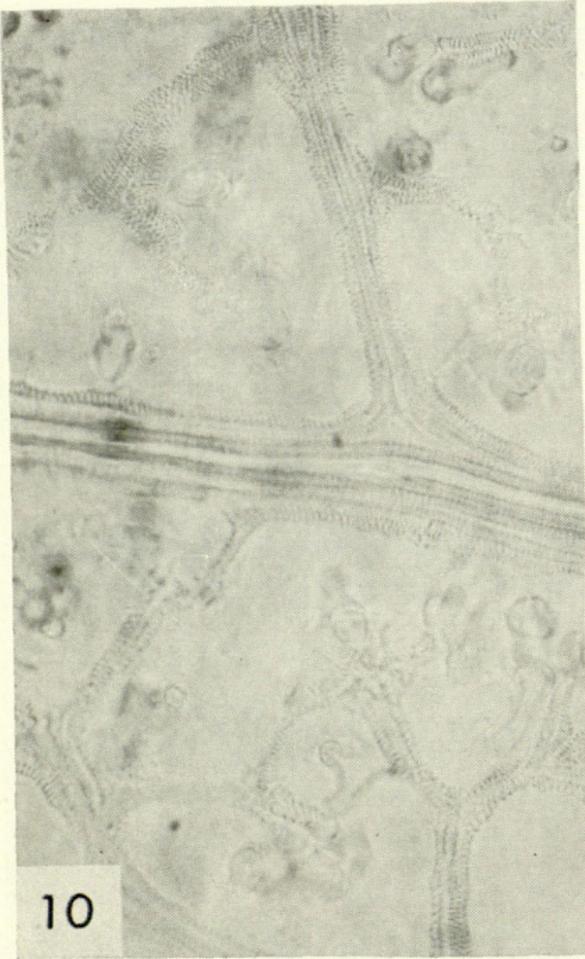
FIGS. 54-57. Foliar idioblastic cells. All, $\times 260$. FIG. 54, *Davilla* sp. (Irwin 5570), transverse section of midrib showing silica-containing cells (arrow). FIG. 55, *Curatella americana* (Irwin 5470), transverse section of midrib showing silica deposits (arrows) and raphide idioblast in upper right. FIG. 56, *Dolioscarpus guianensis* (UC 947180), transverse section of petiole showing sclerotic cells and cuboidal crystals in cortex. FIG. 57, *Dillenia pulchella* (Cult. SING s.n.), arrow indicates enlarged, mucilaginous idioblast in cortical region of midrib.

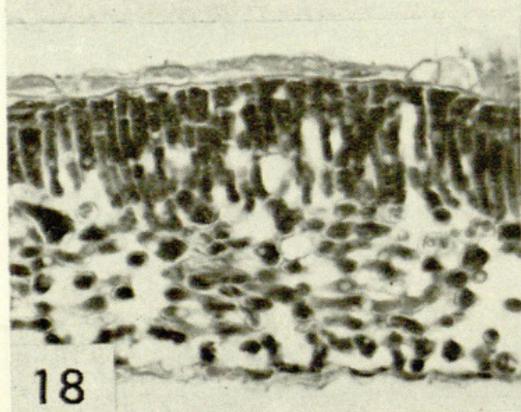
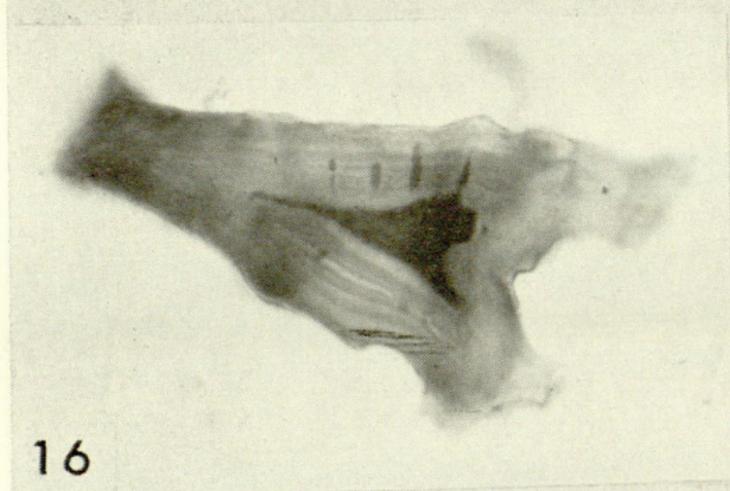
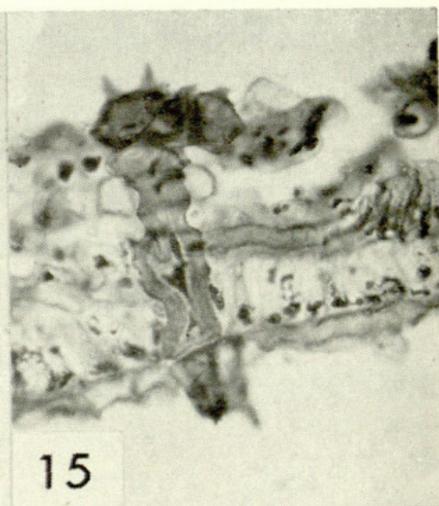
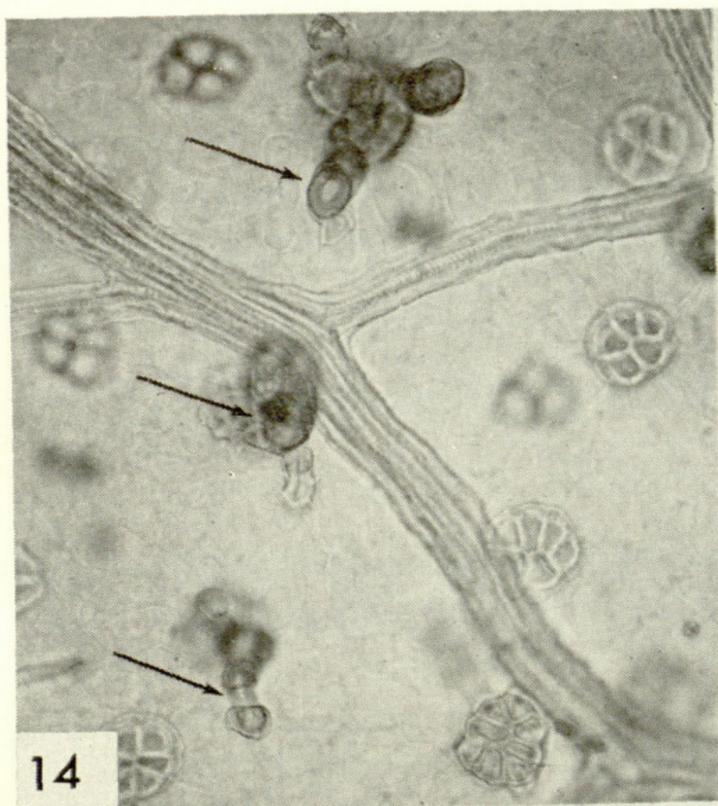
PLATE XII

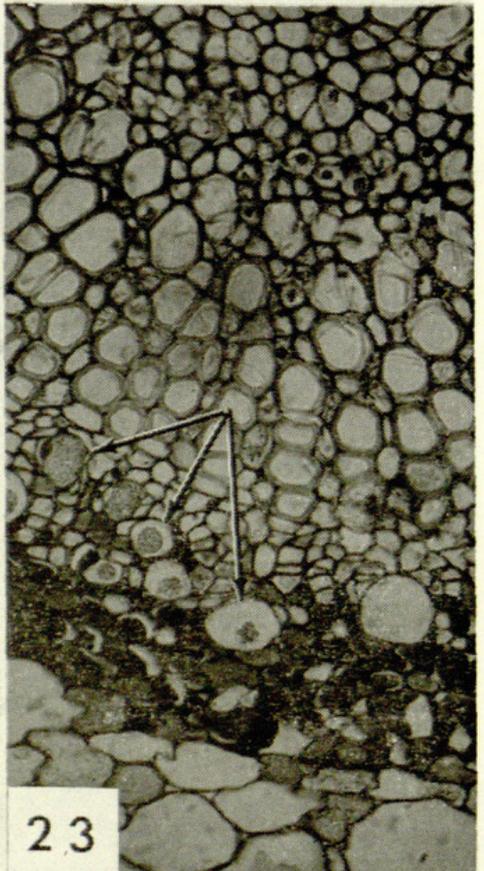
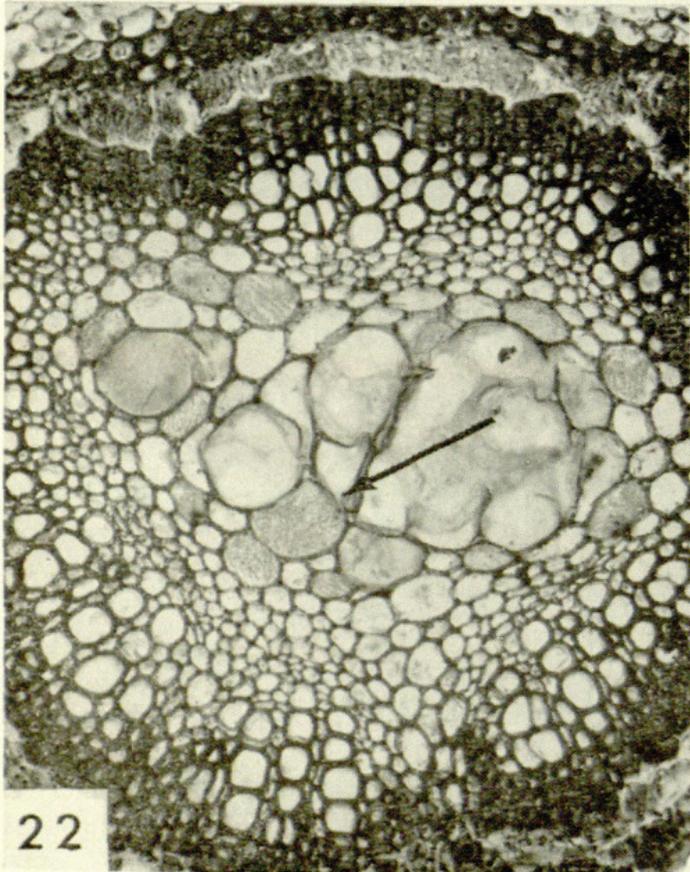
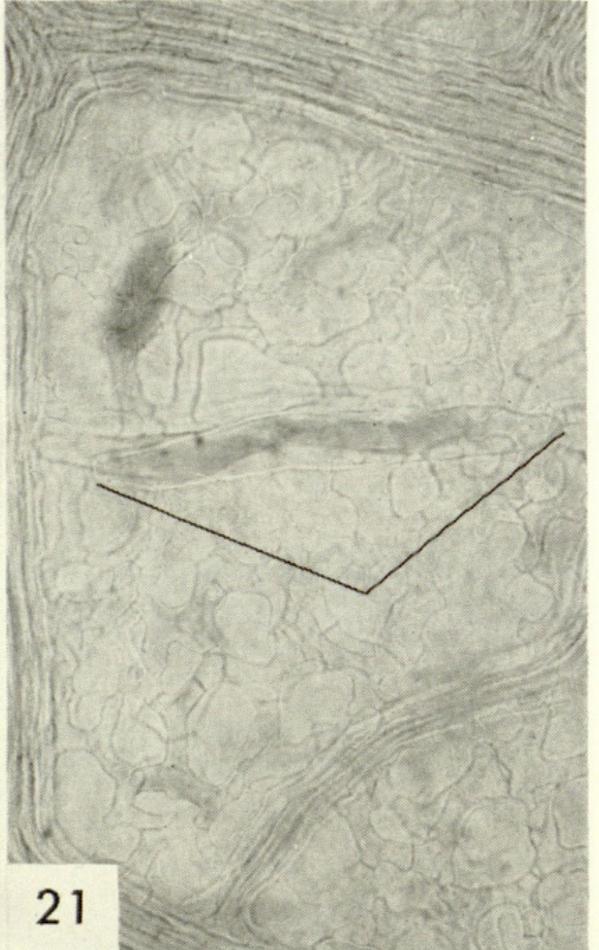
FIGS. 58-61. Foliar trichomes. FIG. 58, *Hibbertia stirlingii* (C. L. Wilson 757), transverse section of lamina illustrating sclerified, fasciculate trichome, $\times 240$. FIG. 59, *H. coriacea* (Humbert 5866), transverse section of lamina showing abundance of curled, unicellular trichomes on lower surface, $\times 160$. FIG. 60, *Dillenia cycloperensis* (Van Royen & Sleumer 5812), cleared leaf showing papillate trichomes restricted to veins, $\times 65$. FIG. 61, *D. philippinensis* (M. Q. Lagrimas s.n., Makiling, Philippines), cleared leaf showing irregular outline of papillate hairs and their general distribution over surface of lamina, $\times 160$.

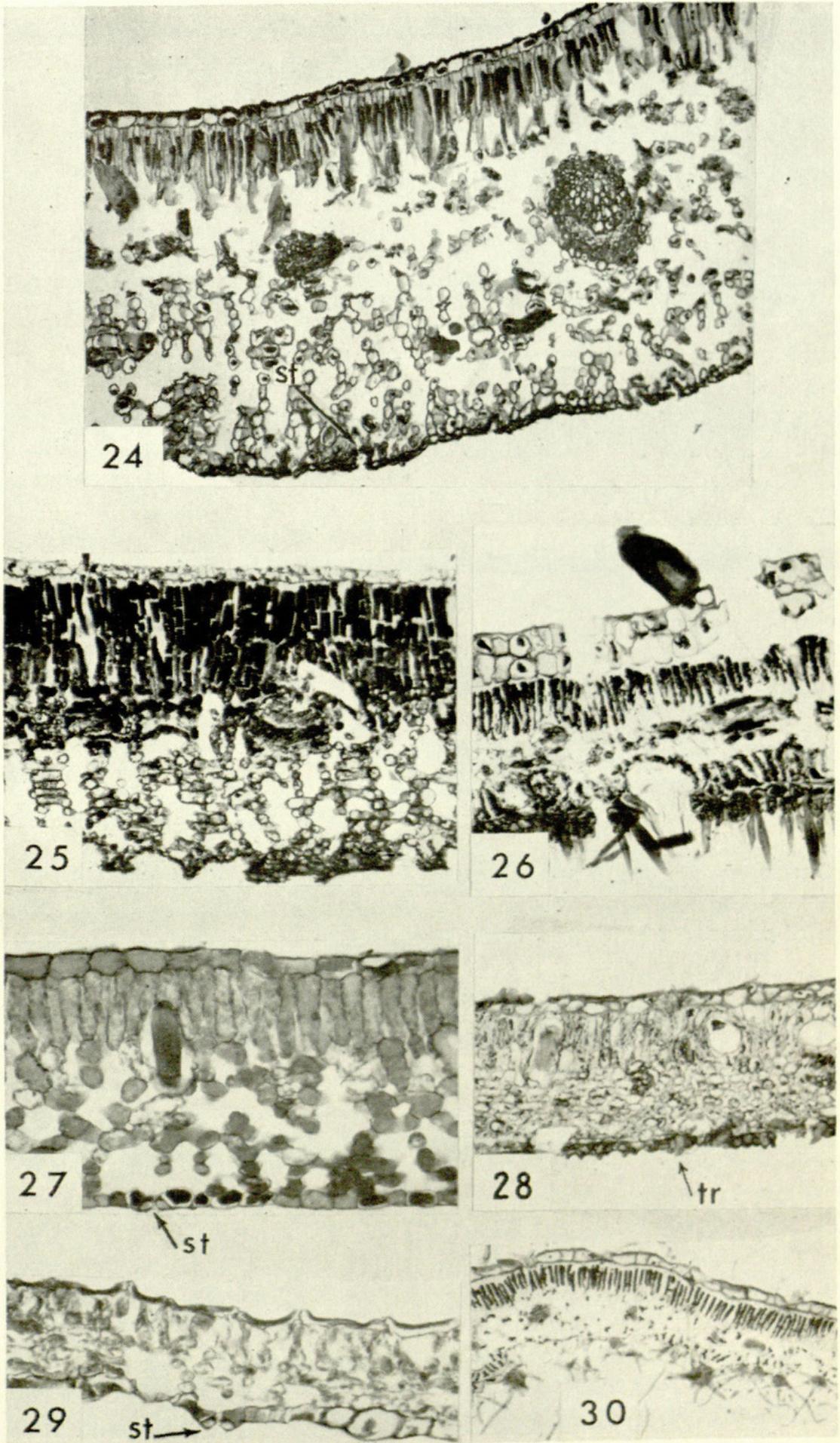




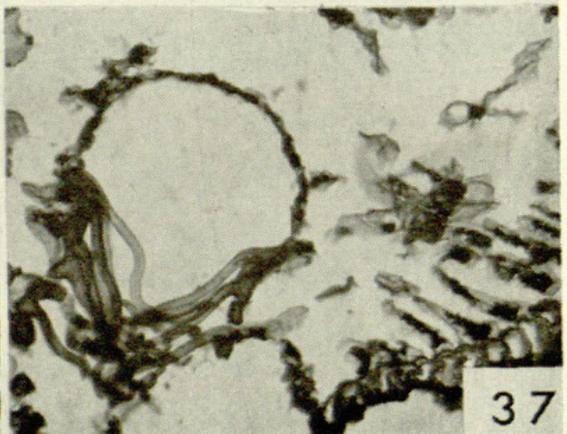
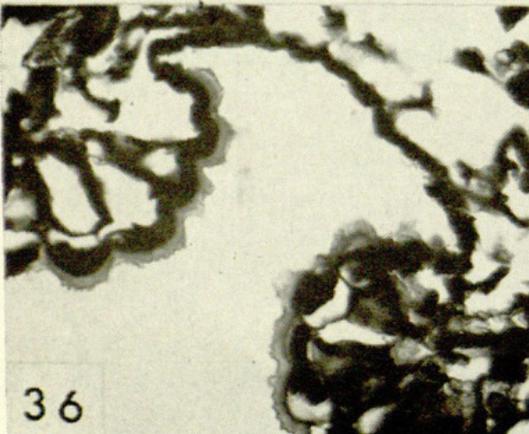
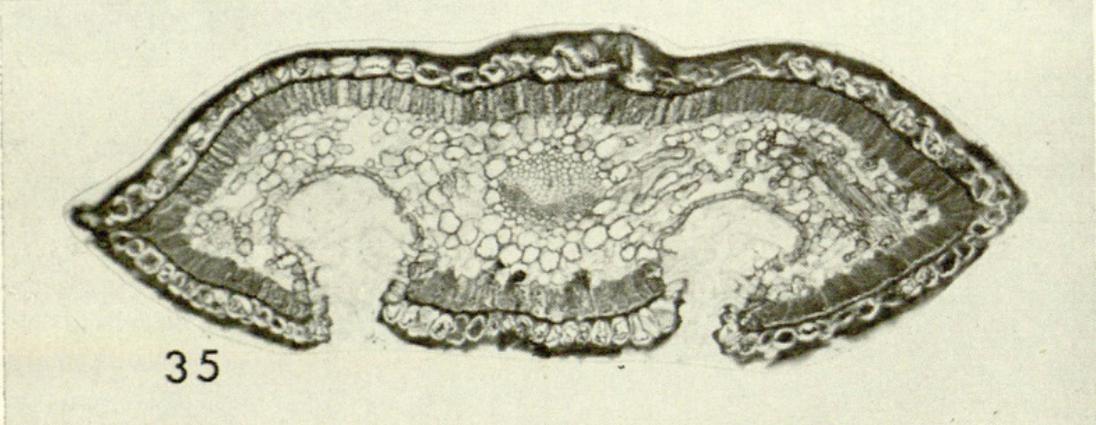
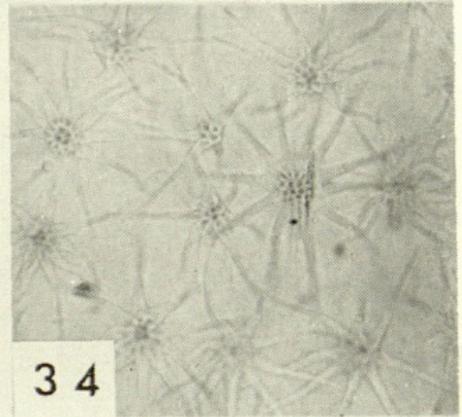
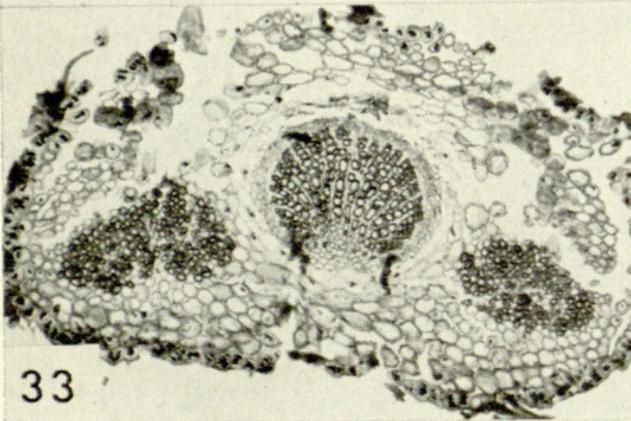
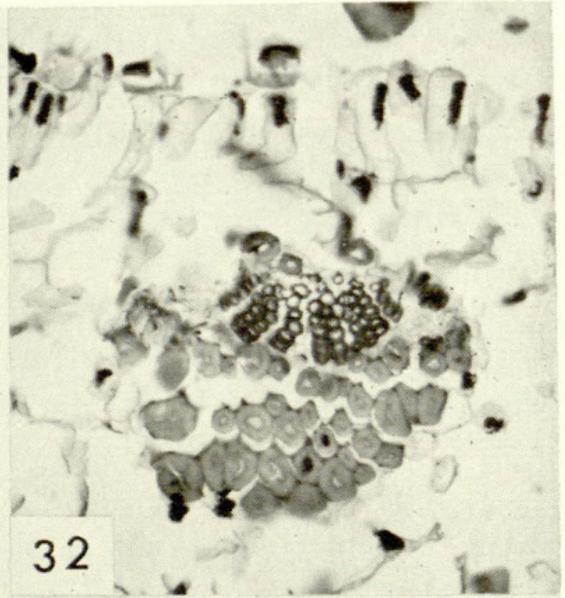
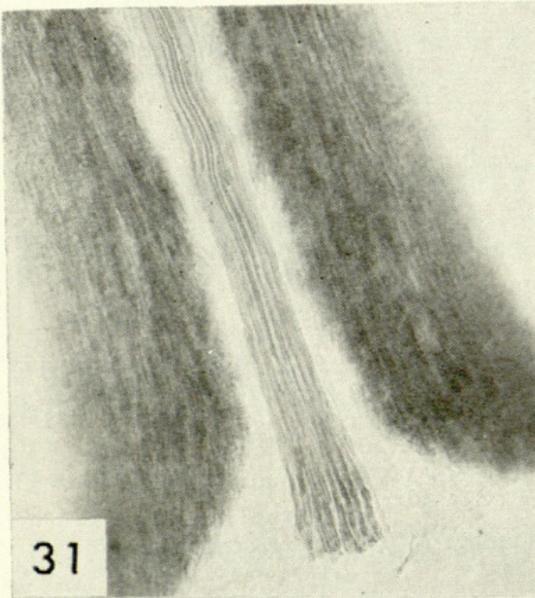


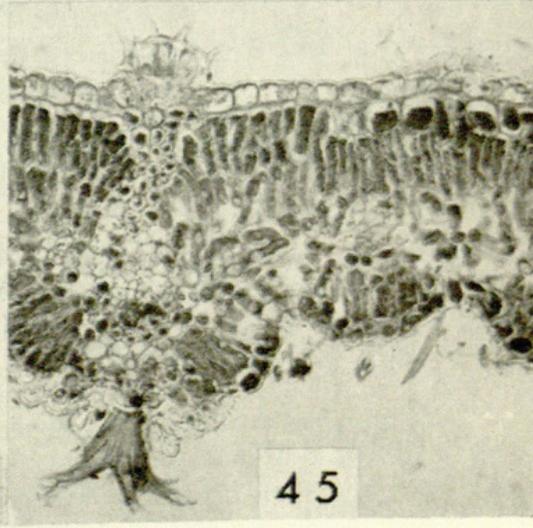
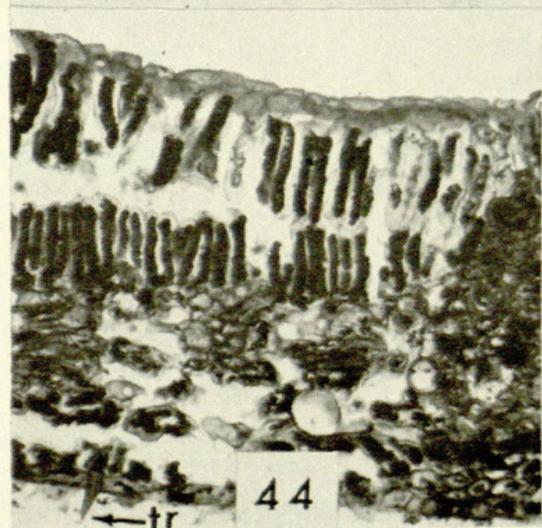
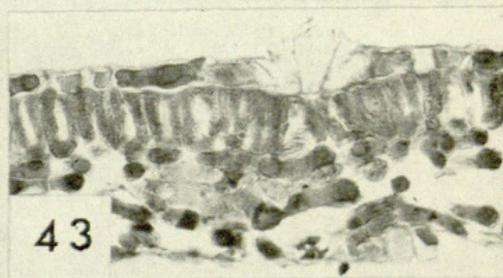
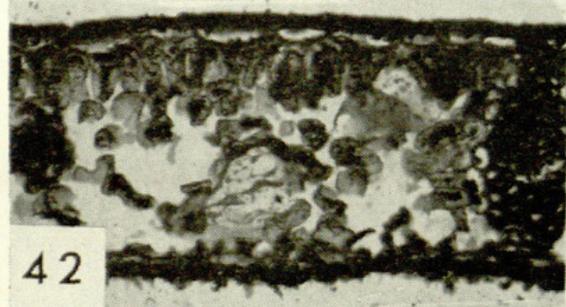
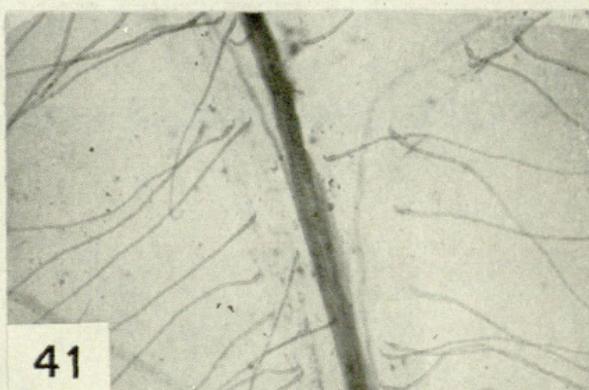
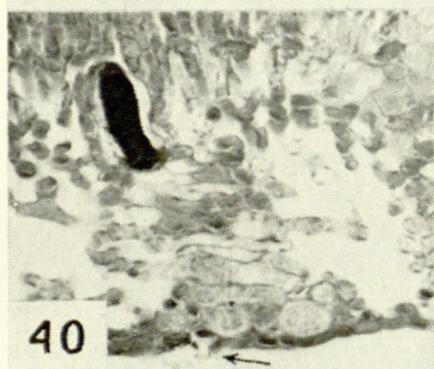
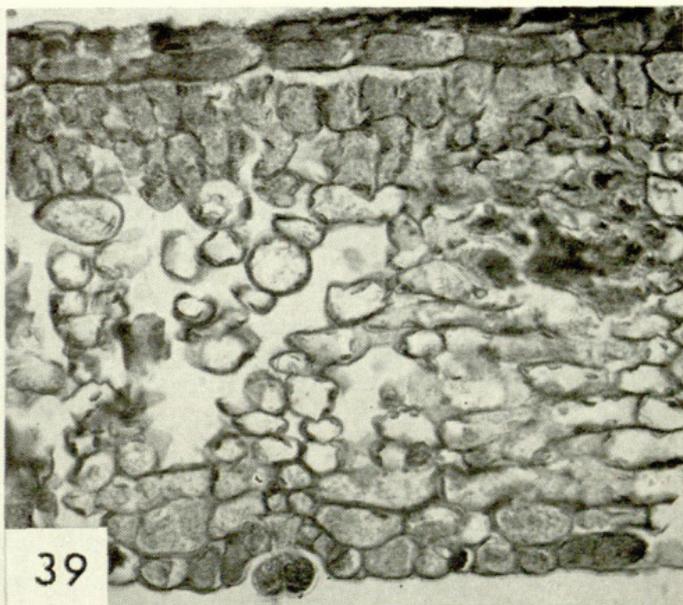
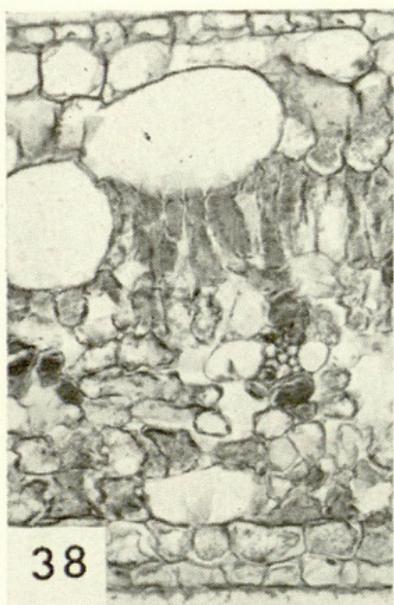


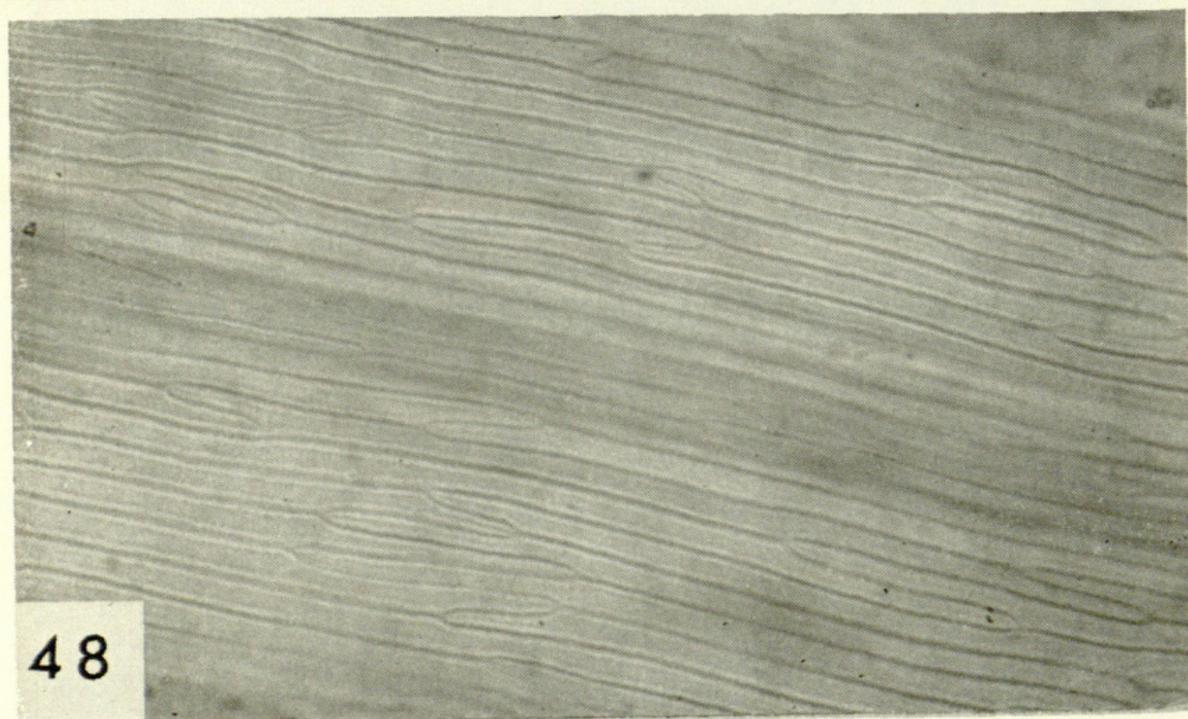
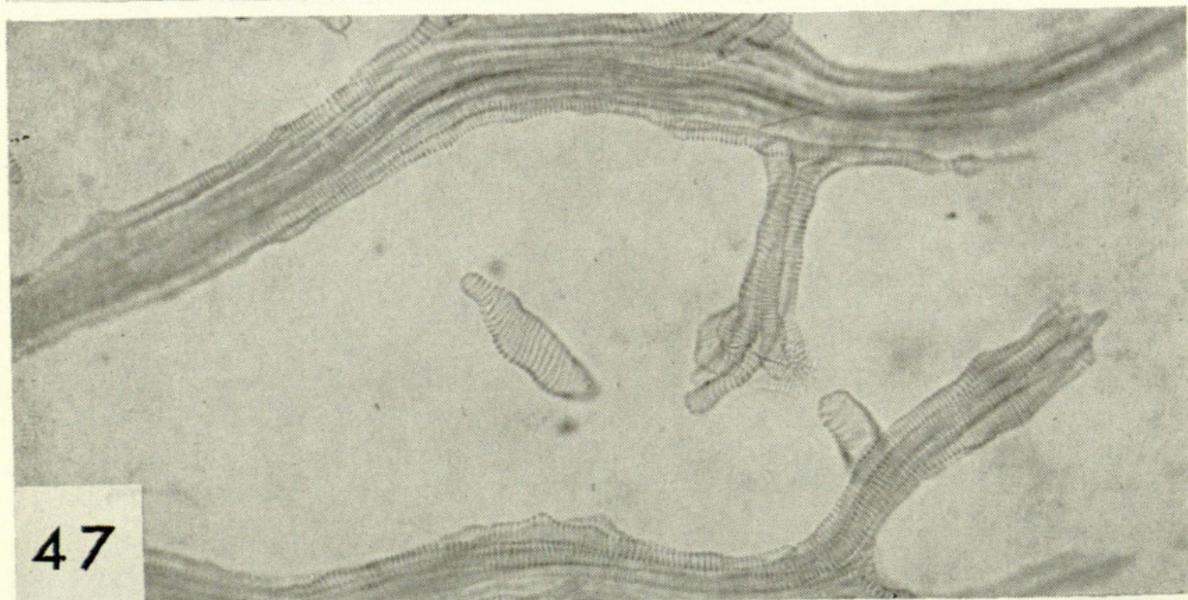
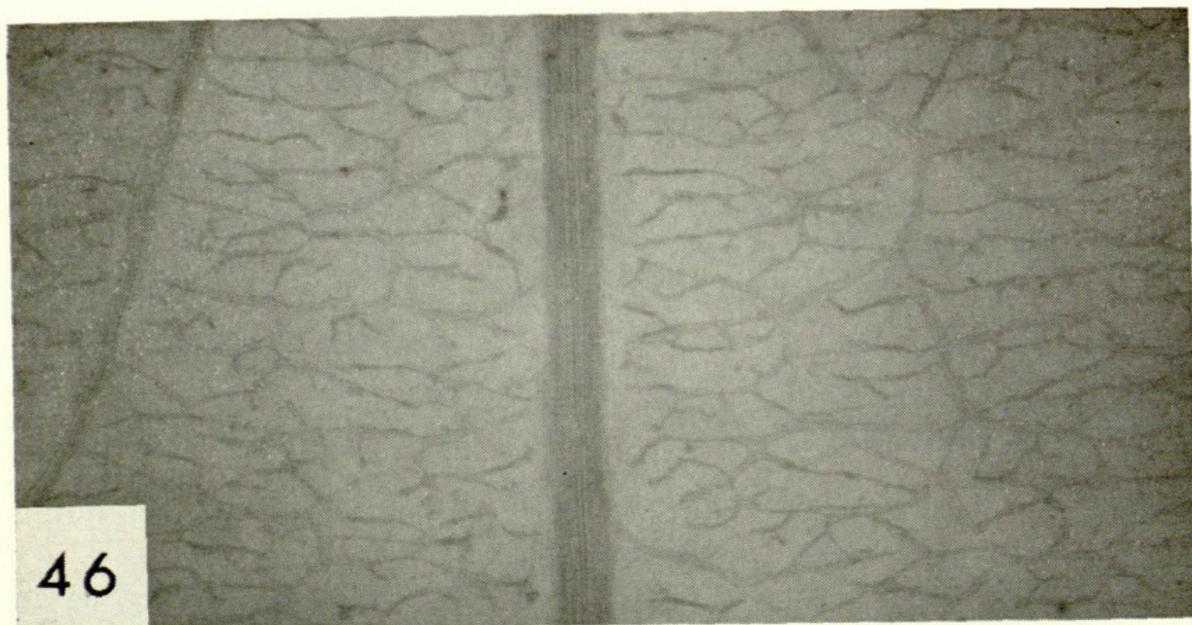


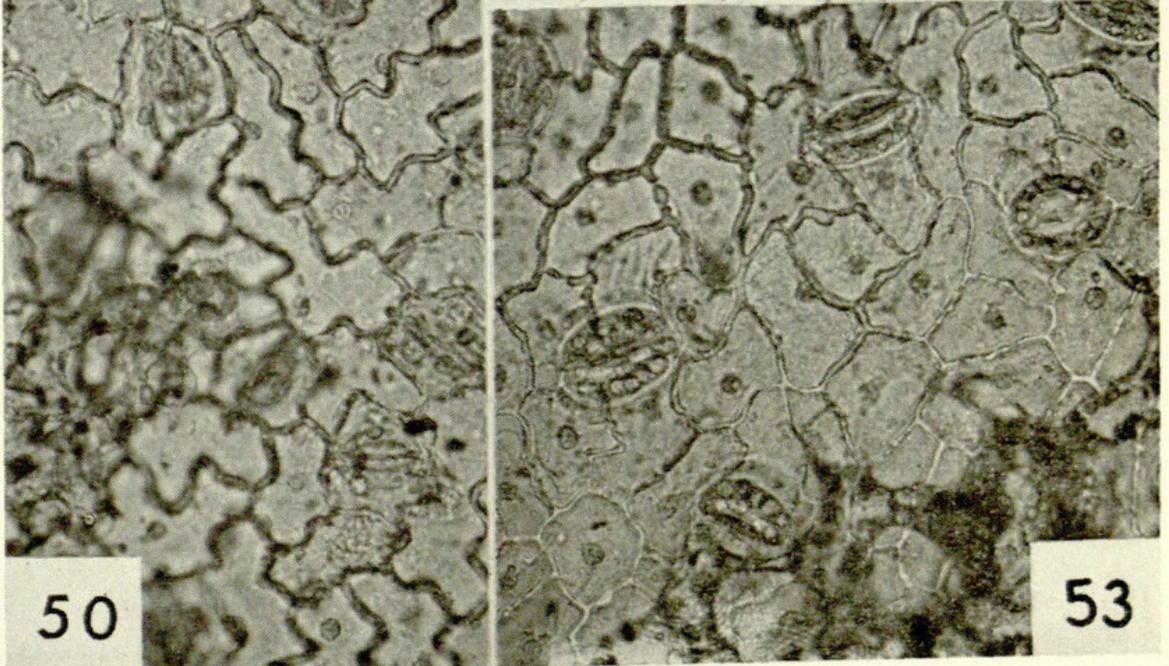
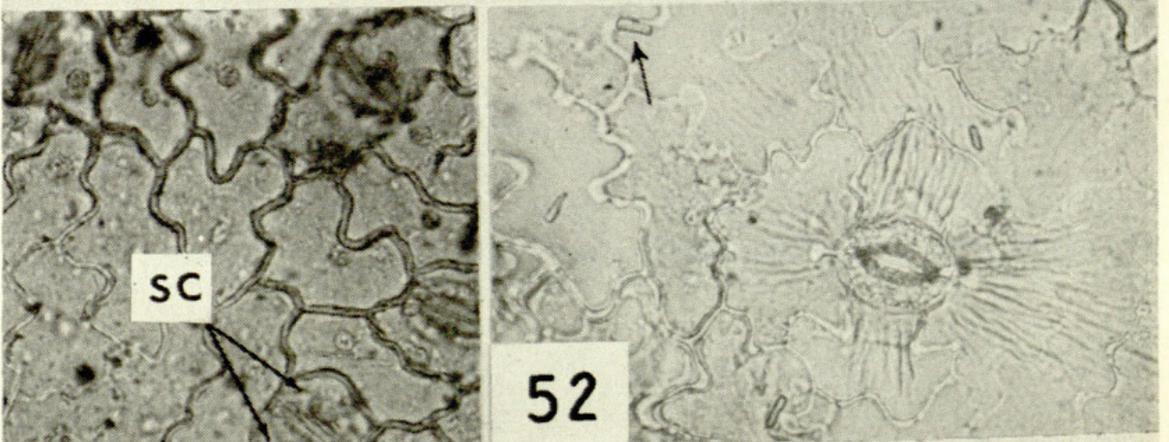
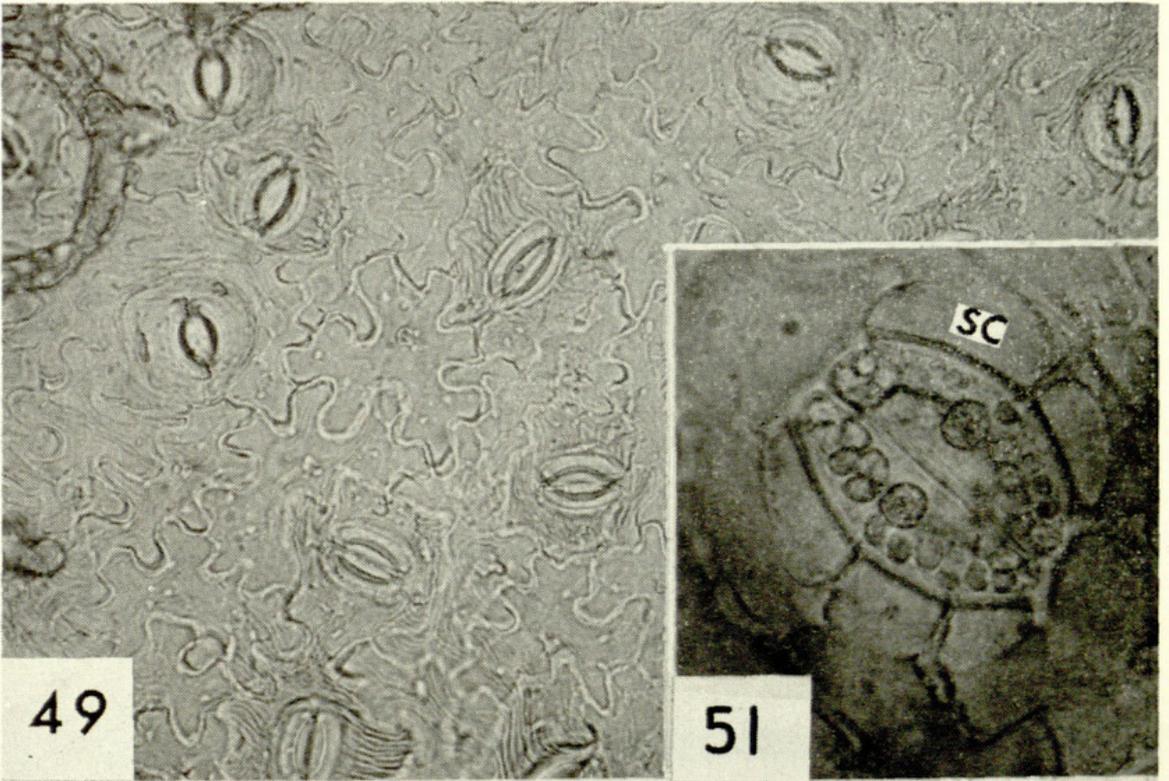


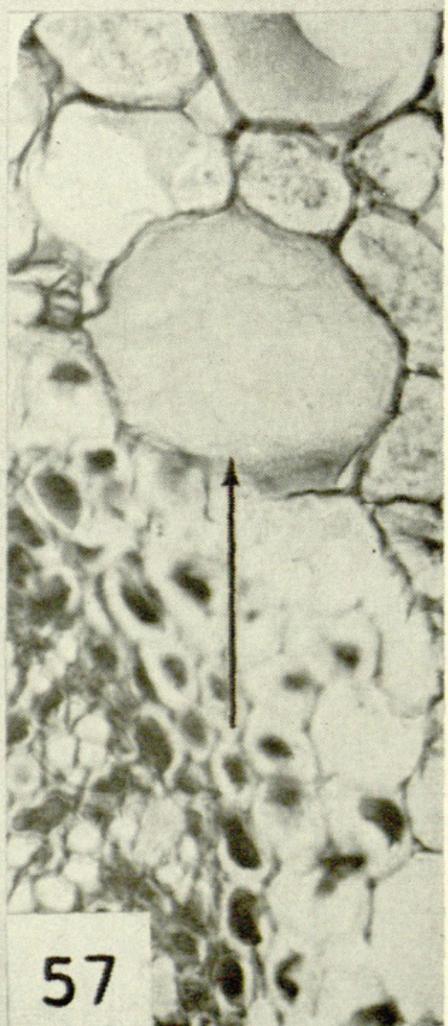
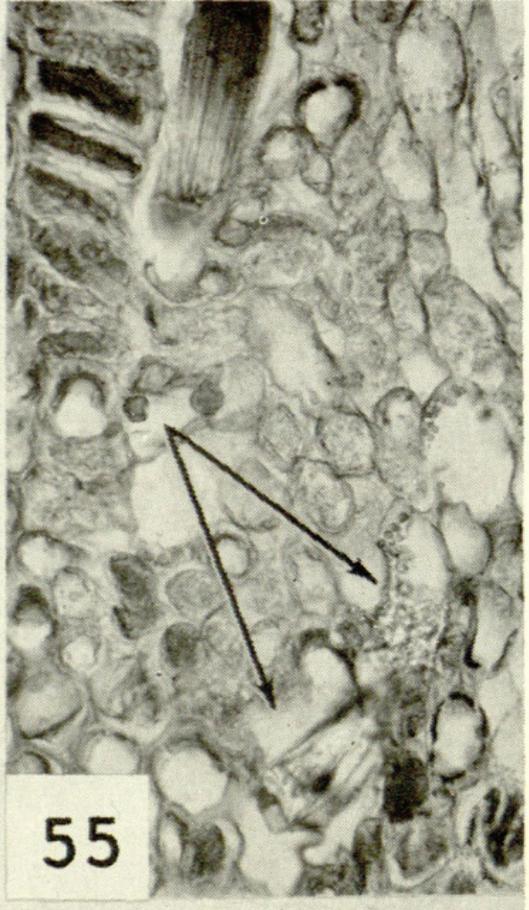
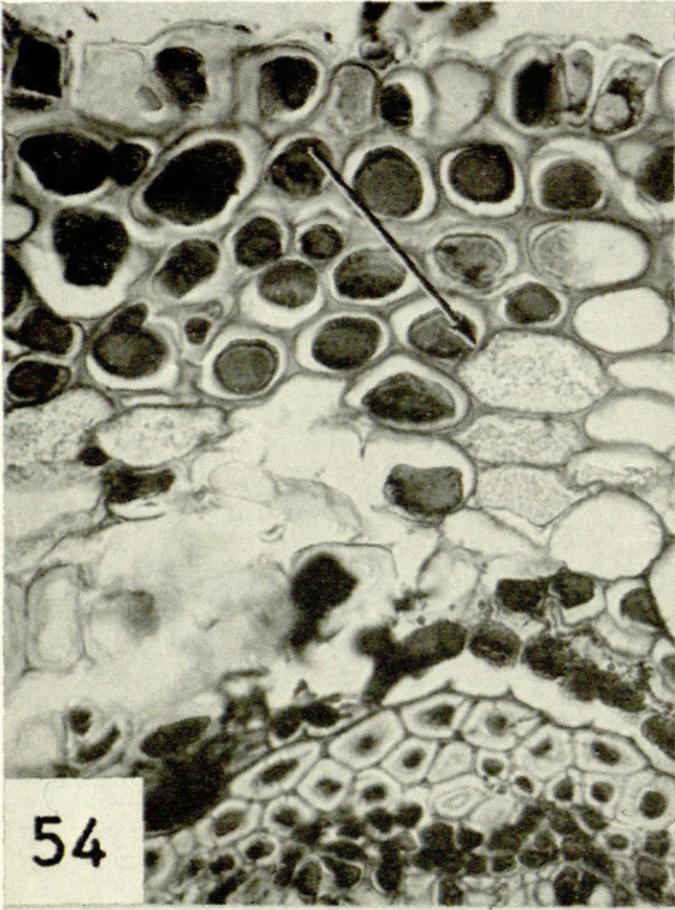
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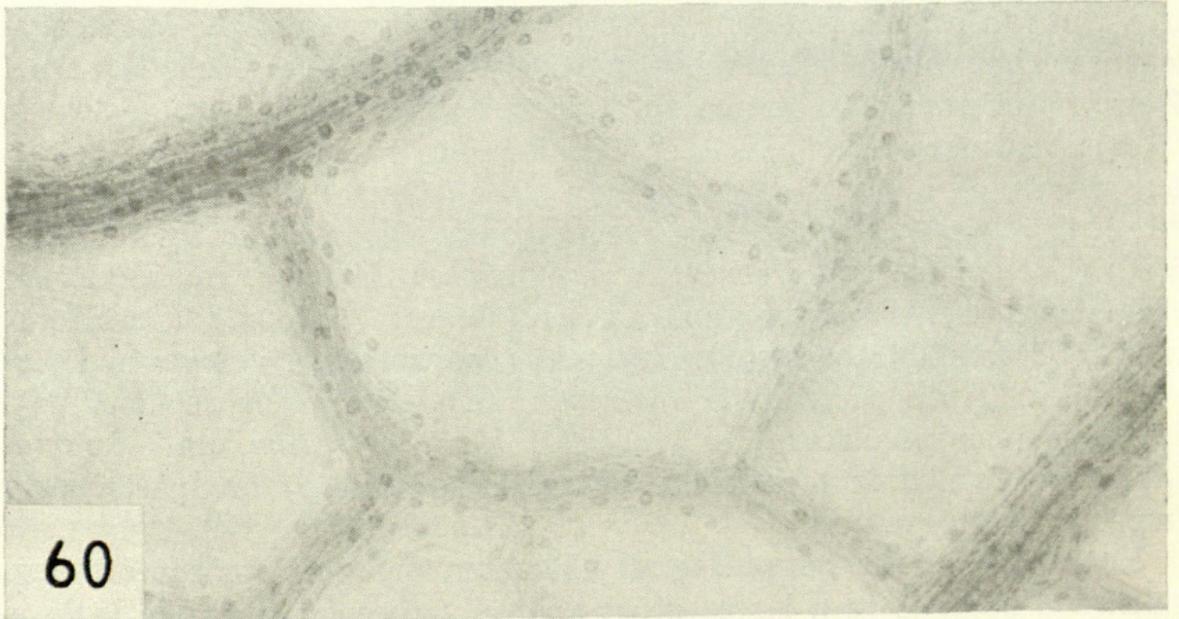
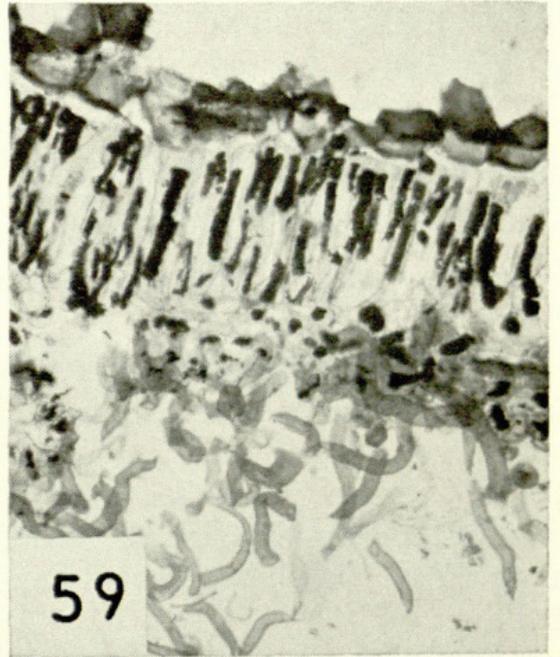














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