HISTOLOGICAL STUDY ON THE TENDRIL OF PARTHENOCISSUS TRICUSPIDATA

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Abstract: The arrangement of the tissue systems and histology of the stem and tendril of *Parthenocissus tricuspidata* (Sieb. & Zucc.) Planch. have been studied. The arrangement of the tissue systems in the stem is fundamentally the same as that in both stalk and holdfast of the tendril. The stem possesses a rather large amount of ground tissue in comparison with other tissues. The tendril stalk has a less amount of living cells, but a larger amount of xylem. The xylem is reduced in the holdfast. The peculiar development of the epidermal cells on the attached surface of the holdfast has also been described. Each epidermal cell on the attached surface of the holdfast elongates and undergoes cell divisions to become a hair-like structure after it comes in contact with a substrate. Other cellular changes also occur in these epidermal cells.

INTRODUCTION

The study of the tendrils of the Vitaceae has been the subject of many investigations. The results of which have appeared in several reports (Millington, 1966; Shah, 1960; Shah and Dave, 1970; Tucker and Hoefert, 1968). The tendril of the Vitaceae, based on phyllotaxy, has been considered to be homologous with the inflorescence (Darwin, 1875; Millington, 1966). It is widely accepted that the tendril in Vitaceae is derived from the axillary branch (Lawrence, 1960). Recently Shah and Dave (1970) concluded that the tendril in some members of Vitaceae is an extra-axillary branch based on their studies of its ontogeny and vascularization.

In order to gain a better understanding of the nature of the tendril, additional evidences from the histology of the stem and some other morphological features have been studied in the present work.

MATERIALS AND METHODS

For the study of external morphology of *Parthenocissus tricuspidata* (Sieb. & Zucc.) Planch., including both tendrils and stems, the authors made careful observations and took pictures of it in its natural habitat and used a dissection microscope for making observations on its minor structures and details.

All the materials for this investigation were collected from the wall of the Herberium of the Department of Botany, National Taiwan University between November 1968 and July 1970. The materials for the anatomical study were collected

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in the morning and fixed in formalin-acetic acid-alcohol (FAA) (Johanson 1940), embedding in paraffin after dehydration by TBA (tertiary butyl alcohol) series. Sections were made at the thickness of 8–10 μ by a rotary microtome, stained with simplified safranin-fast green schedule and mounted in Canada Balsam. In case the materials were too hard to be sectioned, in order to secure good sections, softening after embedding was necessary. This was commonly done by slicing away the paraffin to expose one side of the embedded object, and then soaking it in 1:1 50% alcohol and 50% glycerol solution at 40°C for at least one month. If the deeper part of the specimen had not become completely softened, the rest of the block was treated again in the same manner.

For the study of cell elements in the xylem, materials were cut into pieces about the width of a match and 1 cm long, and then macerated in 1 part superoxal, 4 parts distilled water and 5 parts glacial acetic acid in the oven at approximately 56°C for about 7 days. The macerated tissue was then dehydrated with ethyl alcohol, stained with safranin and mounted in Canada Balsam.

RESULTS

I. External morphology

Parthenocissus tricuspidata is a deciduous vine growing in Taiwan as well as in many other parts of the world, and is mostly cultivated as an ornamental plant. The plant breaks out from its dormancy about the middle of April and begins a new growing season. Young tendrils and leaves develop on the newly formed stems. The newly borne leaves are simple, coarsely serrate and ovate, whereas those which develop from the old stems are consistently 3-lobed to trifoliate, and coarsely serrate with accuminate apices. The middle leaflets appear to be obovate and the lateral ones are obliquely and broadly ovate. Tendrils are borne on the opposite sides of the leaves at the nodes and differ from the leaves in their appearance (Fig. 1). Neither stipule nor stipule-like structures have been found at the base of the tendrils (Fig. 2), whereas two stipules are definitely located opposite the base of each leaf. Each tendril is made up of a main axis and 5 to 9 tendrillets alternately attached to the main axis.

The tips of the young tendrillets are slightly swollen and free from the substrate (Fig. 1a). As the tendrils develop, the tip of each tendrillet becomes a somewhat circular sucker-like holdfast by gradually increasing in size (Fig. 1b). Finally they adhere to the substrate. The holdfast bearing tendrils live only a few months and wither in the same growing season. The color of the whole tendril including holdfasts is green and turns brown as it withers. But the holdfasts still remain attached very tightly to the substrate and serve as an excellent anchors until the new tendrils are formed (Fig. 1c). There is a minute stipule-like scale at the base of each tendrillet (Figs. 1a, 1b). These scales are forked at the tip and pink in

Fig. 1. Tendrils in their natural habitat, ×1.3.
a, young tendrils, notice the scale at the base of each tendrillet.
b, matured tendril, notice the withered scale at the base of each tendrillet.
c, dried tendrils, tightly attached to the wall.

color while the tendrils are young, but they turn brown and fall off when the tendrils grow older.

The arrangement of the branches, tendrils and leaves on the stem follows a certain definite pattern. The leaves are borne alternately at each node of the stem. The tendrils are borne opposite the leaves at every node except those nodes where branches develop. The branch is always formed in the axil of a leaf. Every two tendril bearing nodes is followed by a branch bearing node (Fig. 2c). There is however an exception to the above pattern, if the tendril withers and falls off because of its failure to adhere to the substrate in its early development, the constancy of this order will be broken and a branch will be formed in the leaf axil at the same node and on the opposite side of disintegrating tendril. Thus, the present authors suggest that the existence of the tendril acts as the inhibitor to the formation of branches. This inhibition is eliminated only after tendrils wither or fall off. In general, branches are always borne in the leaf axils, and not on the side opposite to the leaves. Another interesting phenomenon is that the tendrils never become attached to the stems, leaves or other parts of its own plant. They disintegrate if they are in contact with the plant instead of other substrates.

II. Histology

1. Arrangement of the tissue system

Tendril stalk. Like that in the other vascular plants, the tendril consists of identical three tissue systems: the dermal, fundamental and fascicular tissue systems (Fig. 3a). As seen in transverse section, the outermost layer, the epidermis is one cell in thickness except on the attached surface of the holdfast (Fig. 10) (the epidermis of the holdfast will be described in a later paragraph). The outer tangential wall of these uniseriate epidermal cells is covered with a thin cutical membrane. A few stomata have been found. The cortical cells which are located immediately beneath the epidermis are in contact with the guard cells (Fig. 8d), therefore they would be non-functional in stomatal opening. All the cells of the outermost layer of the cortex, some cells in other part of the cortex and other tissue except the xylem are filled with mucilagenous substances which are strongly chromophilic. The thickly stained character of the outermost layer of the cortical cells disappear gradually as the tendril grows.

The cortex which occupies about half of the radius of the transverse section of the lowest stalk of a mature tendril, is composed of parenchyma cells only. Like that in other members of Vitaceae (Metcalfe, 1957), many mucilage-containing cells and raphid-or druse-containing cells are randomly distributed in the cortex.

The vascular tissue is composed of about fifteen collateral bundles in the lowest stalk of a mature tendril. They become fewer in number as they enter the tip of the tendril. The vascular bundles are compactly arranged side by side, and it is

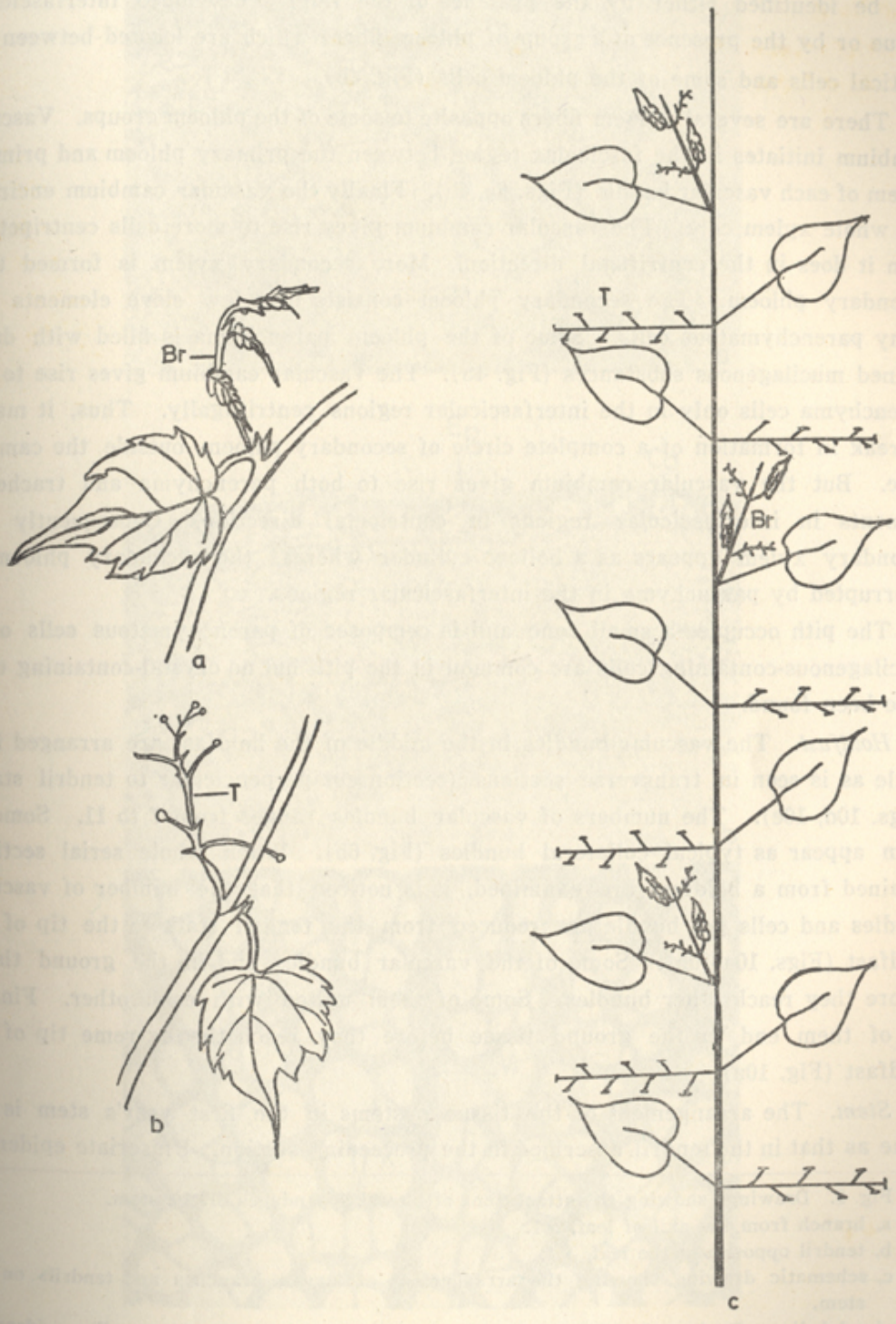


Fig. 2

difficult to distinguish one from the other on the first glance. Each vascular bundle can be identified either by the presence of the faintly developed interfascicular tissue or by the presence of a group of phloem fibers which are located between the cortical cells and some of the phloem cells (Fig. 4b).

There are several phloem fibers opposite to some of the phloem groups. Vascular cambium initiates in the fascicular region between the primary phloem and primary xylem of each vascular bundle (Figs. 3a, 4b). Finally the vascular cambium encircles the whole xylem core. The vascular cambium gives rise to more cells centripetally than it does in the centrifugal direction. More secondary xylem is formed than secondary phloem. The secondary phloem consists of a few sieve elements and many parenchymatous cells. Some of the phloem parenchyma is filled with dark-stained mucilagenous substances (Fig. 4b). The vascular cambium gives rise to the parenchyma cells only in the interfascicular regions centrifugally. Thus, it makes a break in formation of a complete circle of secondary phloem outside the cambial zone. But the vascular cambium gives rise to both parenchyma and tracheary elements in interfascicular regions in centripetal direction. Consequently the secondary xylem appears as a hollow cylinder whereas the secondary phloem is interrupted by parenchyma in the interfascicular regions.

The pith occupies a small zone and is composed of parenchymatous cells only. Mucilagenous-containing cells are common in the pith but no crystal-containing cells have been found.

Holdfast. The vascular bundles in the middle of the holdfast are arranged in a circle as is seen in transverse sections (section cut perpencicular to tendril stalk) (Figs. 10d, 10e). The numbers of vascular bundles ranges from 7 to 11. Some of them appear as typical collateral bundles (Fig. 6b). When whole serial sections obtained from a holdfast are examined, it is noticed that the number of vascular bundles and cells per bundle are reduced from the tendril stalk to the tip of the holdfast (Figs. 10a–10h). Some of the vascular bundles end in the ground tissue before they reach other bundles. Some of them united with each other. Finally all of them end in the ground tissue before they reach the extreme tip of the holdfast (Fig. 10a).

Stem. The arrangement of the tissue systems in the first year's stem is the same as that in the tendril described in the preceeding section. Uniseriate epidermis

Fig. 2. Drawings showing the attachment of lateral appendages of the stem.
a, branch from the axil of leaf, ×1.
b, tendril opposite to the leaf, ×1.
c, schematic drawing showing the arrangement of leaves, branches and tendrils on the stem.
Key for labeling: Br, branch; C, cortex; Ca, cambial zone; Co, collenchyma; Ep, epidermis; Mu, mucilagenous cell; P, pith; PF, phloem fiber; Ph, phloem; T, tendril; V, vascular bundle; Vr, vascular ray; X, xylem.

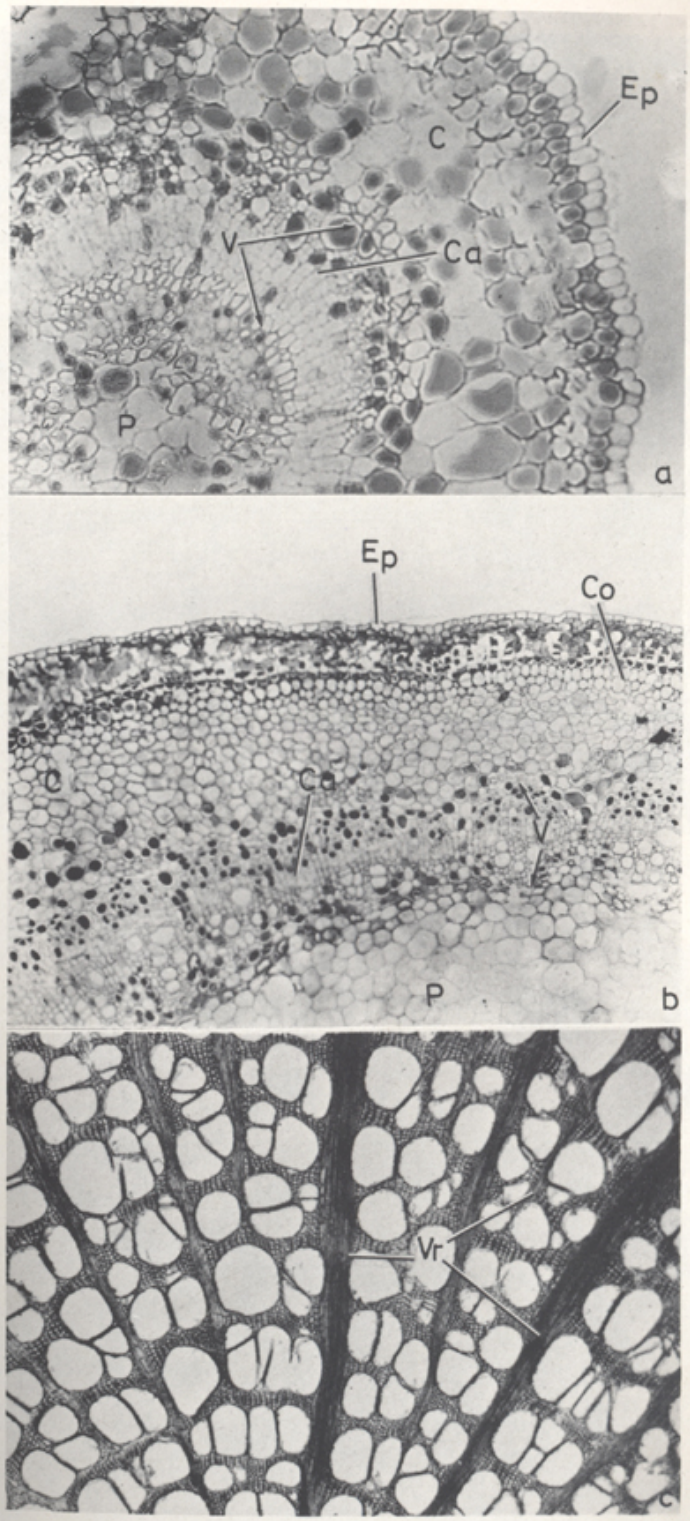


Fig. 3. Photographs showing the transverse sections of tendril stalk (a), and stem (b) at the same stage of development, ×125. (c) Transverse section of an old stem, showing a part of the wood, ×50. See Fig. 2 for labeling.

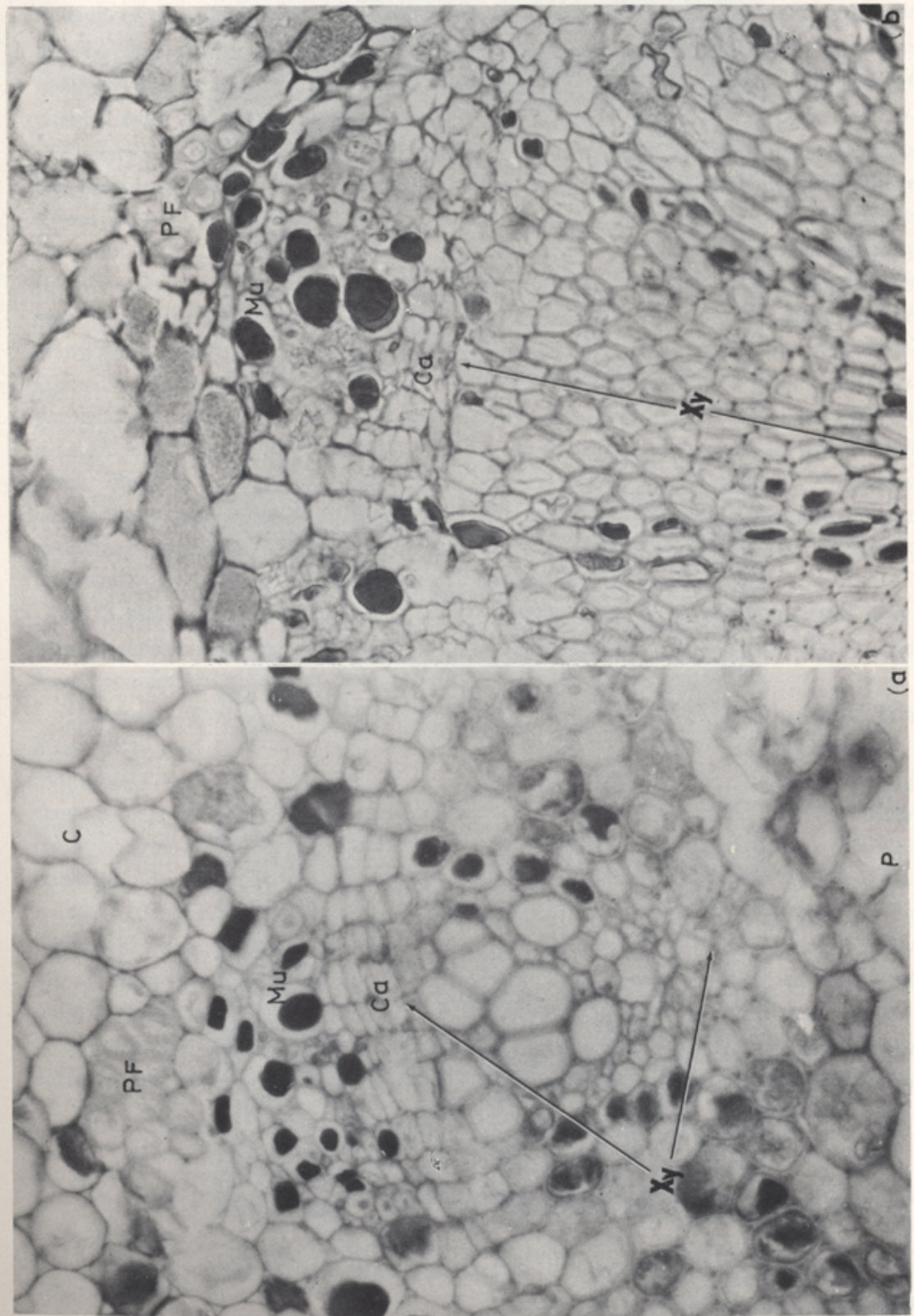


Fig. 4. Transverse sections from the lowest stalk of tendril (b), and stem (a); showing individual vascular bundles, both in their first growing season, all ×270. See Fig. 2 for labeling.

ensheaths all of the tissues of the stem (Fig. 3b). Stomata have not been found in the present investigation. The cortex occupies about one third of the radius of the stem. The outermost cortex which is extensively chromophilic occupies more cell layers than that in the tendril. About eight cell layers of the outermost cortex are darkly stained because of the presence of mucilagenous subtances. Crystal-containing and chromophilic cells are distributed at random in the inner layers of the cortex.

The cells located immediately next to the innermost layer of chromophilic cells are lacunar collenchyma. The collenchyma also forms a complete circle around the inner tissues of the stem and consists of two to three cell layers.

The stem consists of about 26 collateral bundles arranged in a circle. Their indiyiduality can be easily recognized before the secondary growth begins. The primary phloem is composed of several sieve elements, a few companion cells and a large number of the mucilage-containing parenchyma cells (Fig. 4a). The xylem has compactly arranged tracheary elements and several mucilagenous cells which may be thin walled or thick walled.

The vascular cambium develops in its first growing season. The first cambial cells originate both in the interfascicular and in the fascicular regions. It becomes a complete circle as the stem grows. The vascular cambium gives rise to phloem cells centrifugally and to xylem cells centripetally in the fascicular regions. But only parenchyma cells are formed from the cambium both in centrifugal and centripetal directions in the interfascicular regions. It remains as a vascular ray and more rays are initiated inside the fascicular regions as the secondary tissues increase (Fig. 3c).

The pith is of about half of the stem radius. All the cells possess thin walls, and some of them contain mucilagenous substances.

2. Tracheary strands

The tracheary strands run parallel with the stalk of the tendril, but they branch and expand as they enter the holdfast. The shape of the tracheary strand matches that of the external appearance of the holdfast. The tracheary strands more or less unit at the tip of the holdfast (Figs. 5a, 5b). The juvenile tendrillets have less tracheary strands than the mature ones. The xylem matures acropetally. In other words, all the tracheary elements are continuous with that of the base of the tendril. No isolated tracheary elements have been seen in the cleared materials of all the developing tendrils examined.

All of the tracheary elements found in the tendrils show either annular or helical secondary thickenings (Fig. 5c). The tracheary elements in the holdfast are shorter in length than those in the stalk in which some of them are extremely long. Some of them show transverse to oblique end walls but no definite perforation plate has been found. The pattern of pitting on the end walls appear the same as that on the lateral walls of the tracheary elements. Thus, it seemed more reason ble

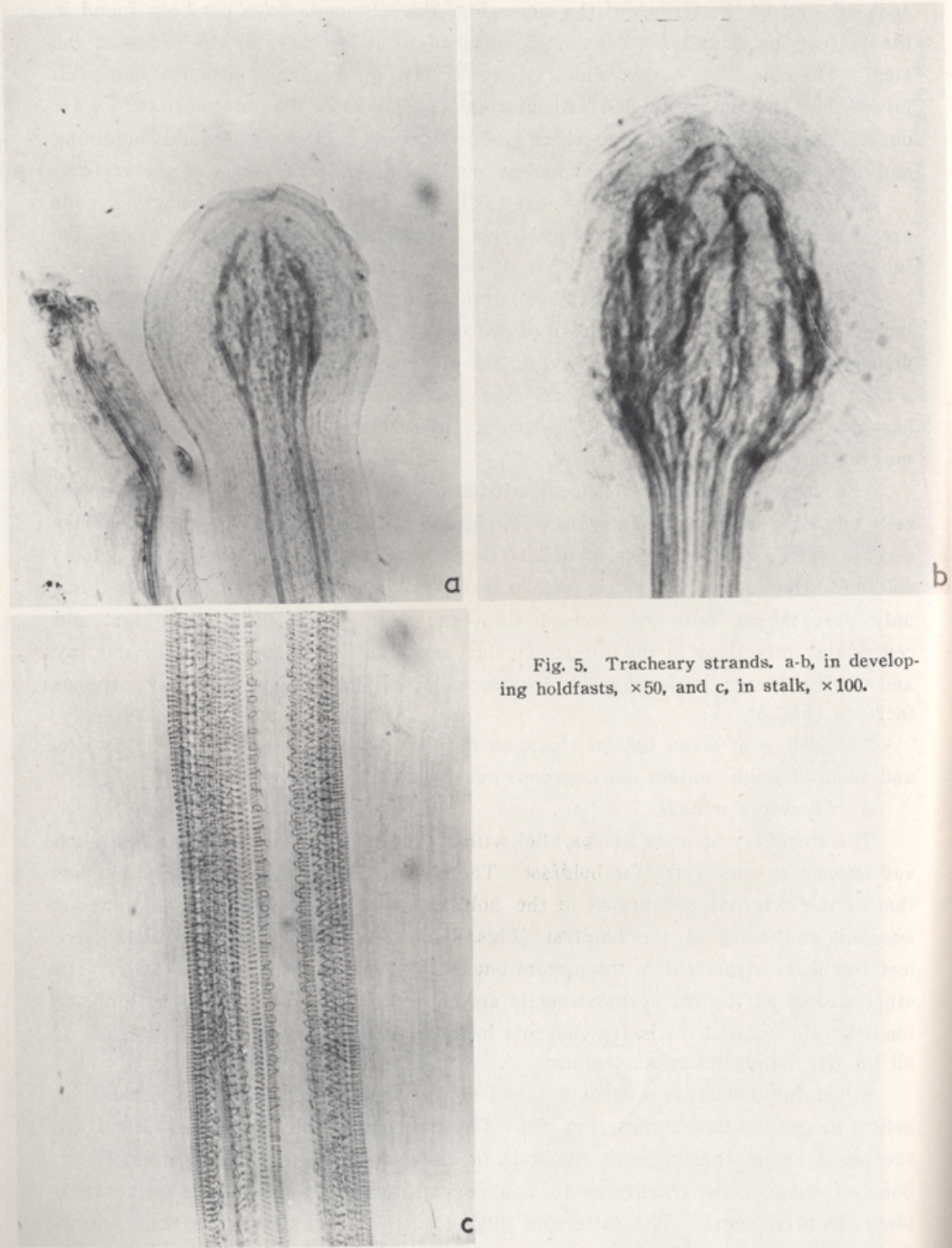


Fig. 5. Tracheary strands. a-b, in developing holdfasts, ×50, and c, in stalk, ×100.

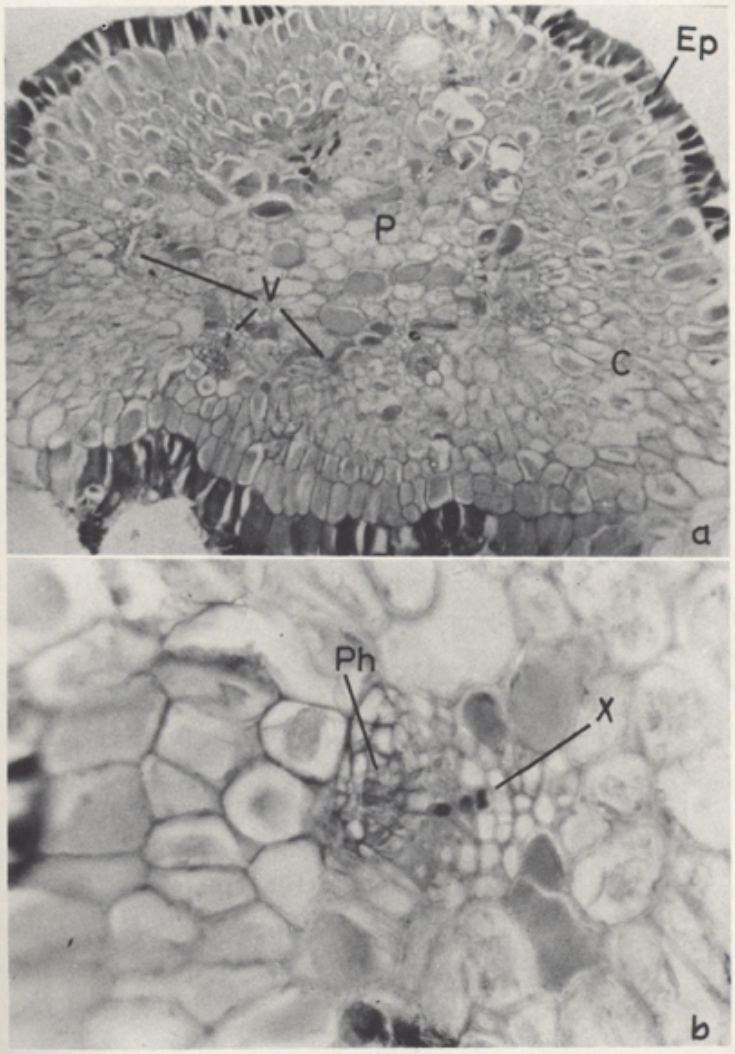


Fig. 6. Transverse section of a holdfast (cut perpendicular to tendril stalk). a, showing the arrangement of vascular bundles in a circle, ×100; b, an enlarged vascular bundle from Fig. a, showing a collateral bundle, ×450. See Fig. 2 for labeling.

to term them tracheids rather than vessel members. No typical vessel members have been found either in stalk or holdfast. In addition to the tracheary elements, another type of lignified cell, *i.e.* fiber tracheid, is present in the tendril. Because of the absence of vessel members the xylem of the tendrils appear homogeneous in transverse section. (Fig. 4b).

The tracheary elements of the stem differ from those of the tendril in the presence of vessel elements. The size of these vessel elements vary from each other some of them are narrow and long whereas others are broad and short. The pattern of pitting in the lateral wall of the vessel element ranges from scalariform to reticulate. The end wall of vessel element is slightly oblique with a small tail to being transverse without a tail. Most of the vessel elements possess simple perforation plates. Scalariform perforation can also be found but rather infrequently. They occur only in those which are narrow and long. The tracheids found in the stem are about the same size as those in the tendril and are very similiar in shape. Fiber tracheids are also present in the stem. No other types of fibers were found.

3. Epidermis of holdfast

The epidermis of the holdfast is one layer of cells in thickness. The epidermal cells are compactly arranged and are elongated in the radial direction as seen in transverse sections, whereas the epidermal cells of its associated tendril stalk are less elongated with their long axis parallel with the long axis of the tendril stalk (Figs. 7c, 7d). Chromophilic substances are conspicuous in all of the epidermal cells, most cells in the subepidermal layer and some of the cells in other parts of the holdfast.

As soon as the holdfasts come in contact with a substrate, the epidermal cells become extremely elongated along their radial direction with the nuclei located near the distal end (*i.e.* near the substrate) of the cells (Figs. 8a, 8b). The elongations that take place in these cells are not at the same rate. The radial walls of the epidermal cells separate from each other as they become elongated, and look like a cluster of hairs. Some of these hair-like epidermal cells protrude into the intercellular spaces of other epidermal cells, and they might twist around each other. Finally the attaching surface of the holdfast is covered by the hairy structure (Fig. 8c). The distal ends of the elongated epidermal cells are more or less enlarged. Thus it appears as club-shaped. The protoplast in the enlarged end is always lighter than that in the slender end (Figs. 8a–8c). Some of the elongated epidermal cells divide unequally. A smaller daughter cell is formed at the distal end and a larger daughter cell at the proximal end. Further cell division may occur in these cells. So that the hairy structure on the attaching surface of the holdfast is epidermal in nature. Each "hair" may be an elongated epidermal cell or a series of cells which are derived from an epidermal cell by farther division or divisions after it has come in contact with the substrate.

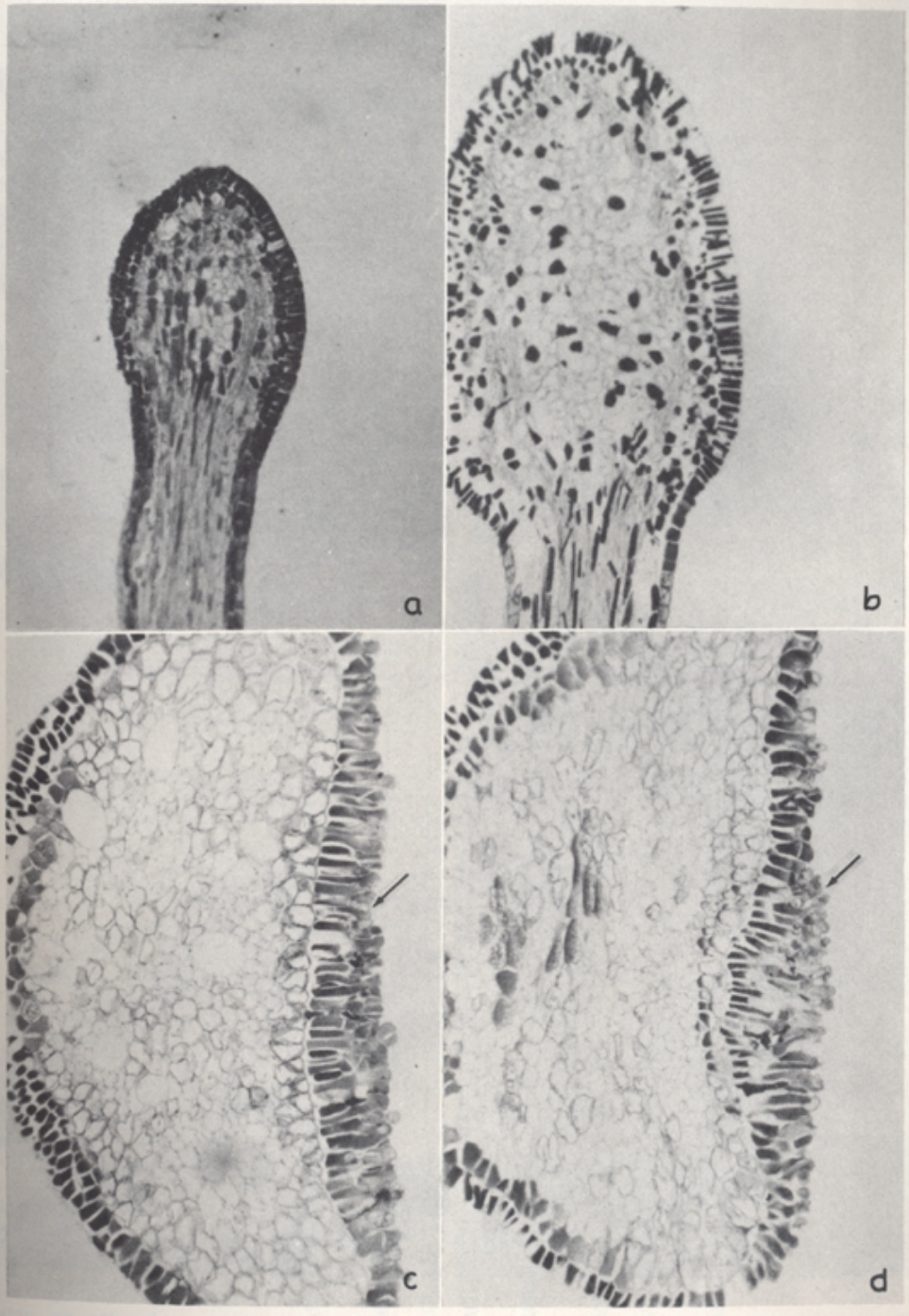


Fig. 7. Photographs showing the early stages of developing epidermal cells on attached surface of holdfasts, all ×100; a and b, epidermal cells are uniseriate and compactly arranged; c and d, some of the epidermal cells elongated and multicellular (arrows). See Fig. 2 for labeling.

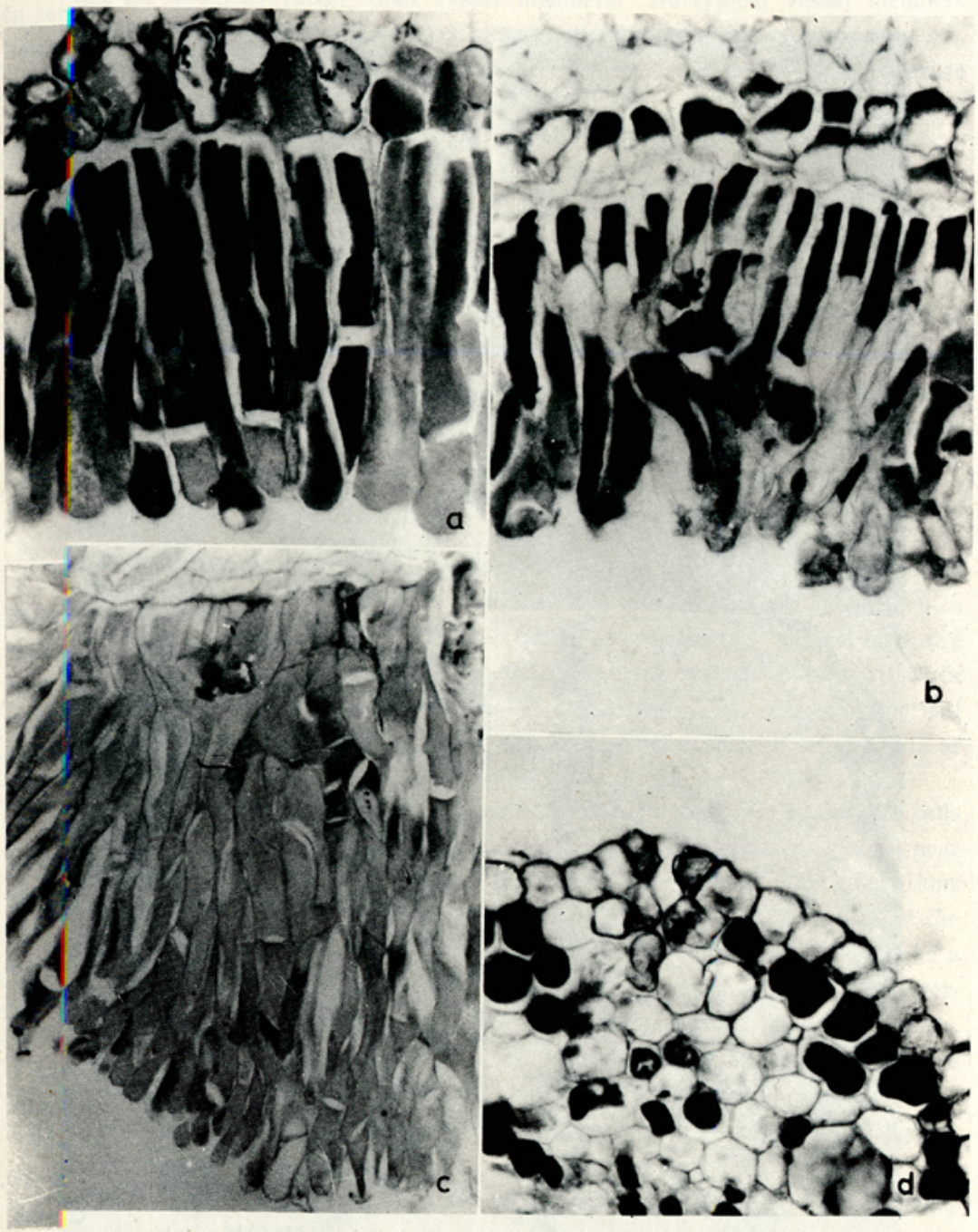
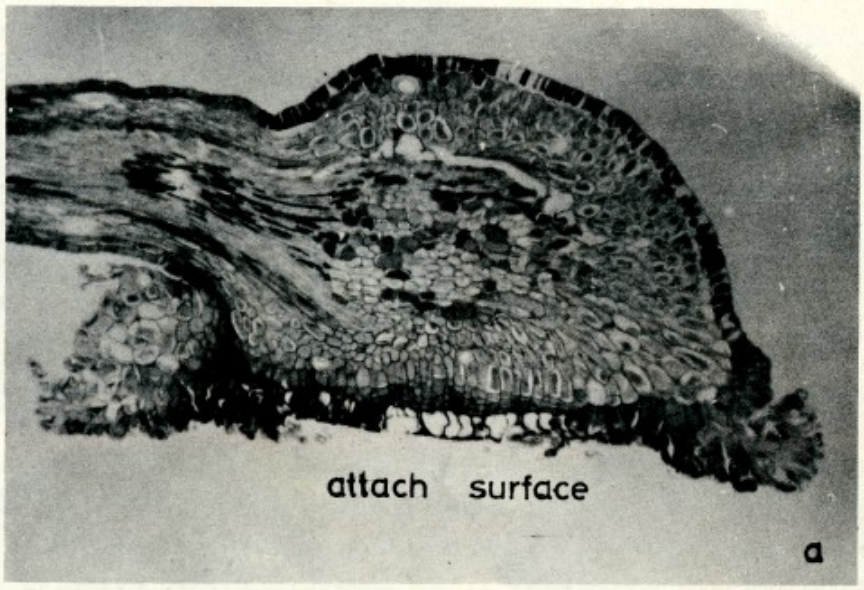


Fig. 8. Photographs showing the later stages of developing epidermal cells on attached surface of holdfasts. a and b, epidermal cells are extremely enlarged, and some of them are bicellular, notice the nuclei are located at the distal ends, ×450; c, from a mature holdfast, most of the cells are multicellular ×200. d, transverse section of tendril stalk, showing the stomata ×250. See Fig. 2 for labeling.



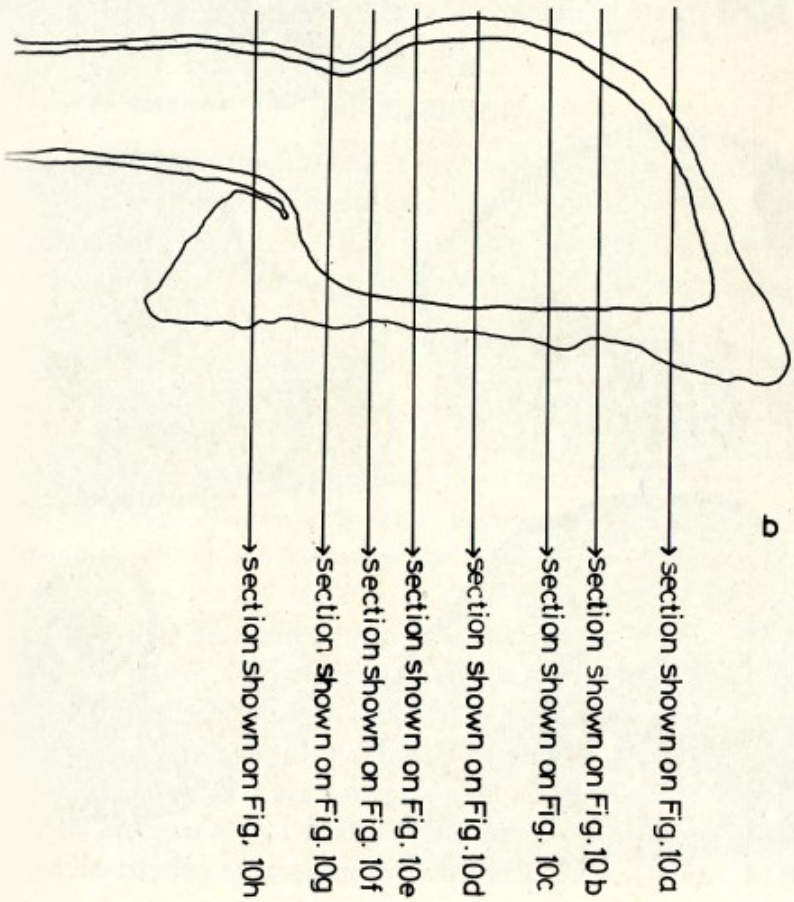


Fig. 9. Median longitudinal section of a mature holdfast, ×50.

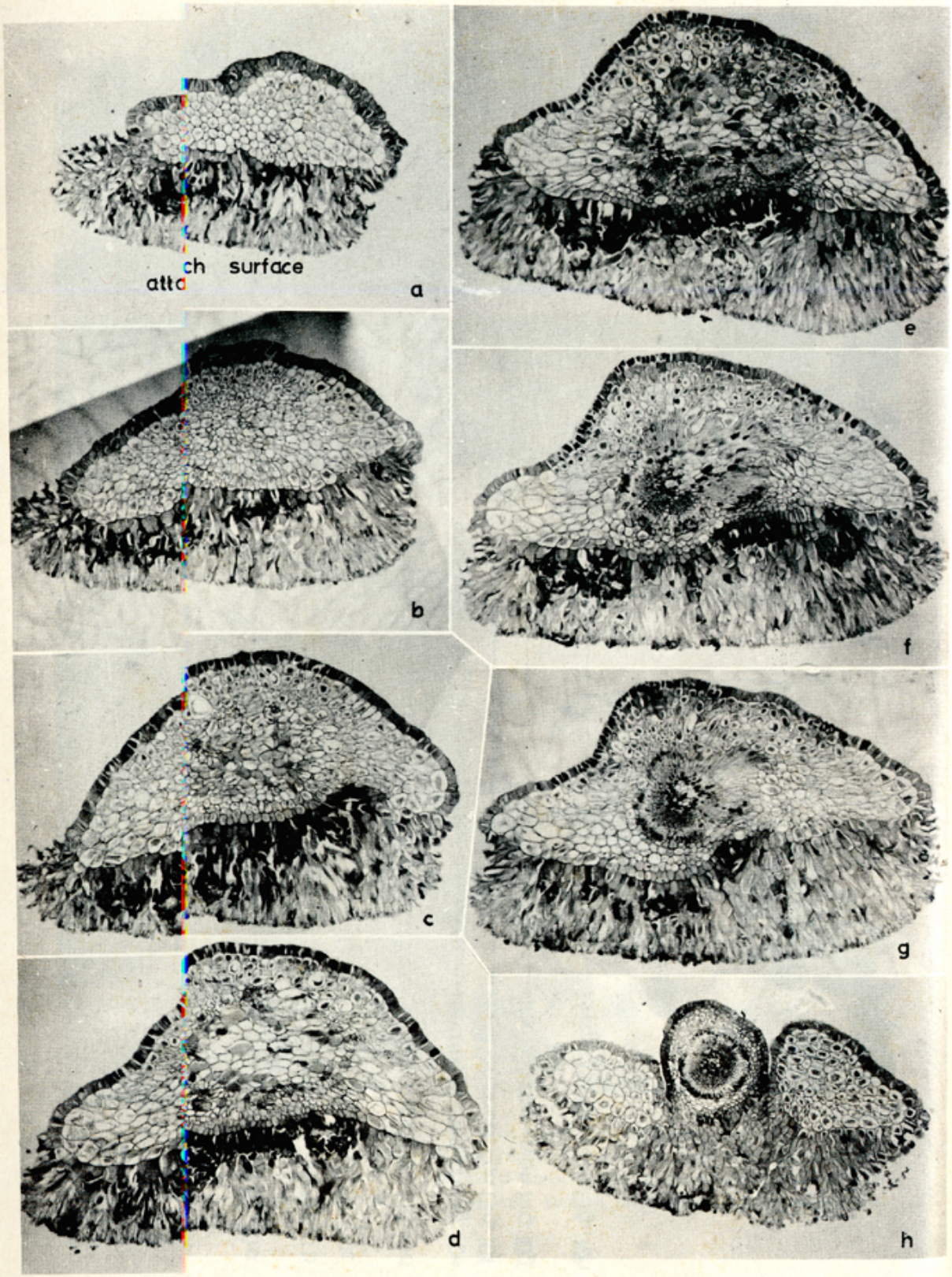


Fig. 10. hotographs showing some of the serial transverse sections (cut in perpendicular to tendril st[illegible]c) from the tip (Fig. 10a) to the base (Fig. 10h) of a mature holdfast. all ×40. labeling.
See Fig. 2 f[illegible]

One to two nuclei are visible in the distal cells of the hair-like epidermal cells. The nucleus is conspicuous and always occupies the central position in the distal cell. The staining nature of the cytoplasm in the distal cell of the hair-like epidermis differs from that in the other cells of the hair-like epidermis. The former is less chromophilic than that the latter.

Since the tendril attaches to any kind of substrate on which microorganisms may grow, various types of microorganisms, such as algae, spores and even young plants of mosses are found. These grow intermingled with the hair-like cells.

Some of the epidermal cells soon cease to divide into long multicellular hairs and remain a one- or few- celled hair, whereas in others they are 5 to 7 celled. The epidermal cells which fail to divide become deeply stained (Figs. 10a–10h). Furthermore, the cortical cells which are located immediately next to the hair-like epidermis divide serveral times periclinally, and the products of these divisions become storied in appearance (Fig. 9a). This storied arrangement of subepidermal cells are conspicuous in the middle on the adhesive side of the holdfast. The peripheral region on the adhesive side of holdfast always bears longer "hairs" which form a complete hollow circle around the edge of the holdfast (Fig. 9a). The hair-like epidermis in its mature stage occupies about two thirds the radius of the holdfast as seen in sections cut perpendicular to the substrate.

DISCUSSION

In the present investigation it has been found that the arrangement of the tissue systems in the stem is fundamentally the same as that in both stalk and holdfast of the tendril (Figs 3a, 3b, 6a). Both stem and tendril develop cambium in the first growing season. But the cambial activity in the tendril stalk ceases as it turns brown. The pattern of the arrangement of the leaves and tendrils on the stem, and of the tissue systems agree with the earlier works that the tendril is a modified shoot or branch (Lawrence, 1960; Millington, 1966; Rendle, 1952; Shah and Dave, 1970).

The tendril lives for only one growing season whereas the stem develops new appendages every year. The tendril stalk possess rather a small amount of parenchyma ground tissue, on the contrary the dead tissue (*i.e.*, xylem) occupies a considerable area of the tendril stalk as is seen in transverse sections (Fig. 3a). This xylem is compactly arranged without vessel elements inside. The presence of the large amount of xylem plays an important role in the mechanical resistance of the tendril after its withering. New appendages are never found occurring on the tendril because of the presence of the small amount of living cells. The living cells are always essential for regeneration as well as other states of the growth.

We found the arrangement of tendrils and leaves of *Parthenocissus tricuspidata* agrees with the description of it given by Shah and Dave (1970). In the present

work it has been found that the branches are also arranged according to a definite order on the main axis as well as the lateral branches (Fig. 2c). It is interesting to notice that tendrils never attach to any part of the same plant on which the tendril grows. They always disintegrate if they come in contact with another part of the same plant. The explanation for this phenomenon may be due to hormone which may be correlated with the epidermal cells on the attached surface of the holdfast.

The epidermal cells on the attach surface of the holdfast alter their morphology as soon as they come in contact with any substrate. It is not difficult to imagine that the extensive elongation of the cell brings about further cell division. But what causes the elongation of the cell, the enlargement of the distal end of the cell, and the peculiar pattern of the distribution of the cell contents? These cellular changes never occur in the epidermal cells on the back surface (non-attached surface) of the holdfast. Numerous stomata have been seen on the non-attached surface of the holdfast. But no hydathode-like structures are found. The tendril of *Vitis vinifera* bears both hydathodes and stomata ("water-pore" by Tucker and Hoefert, 1968). The peculiar staining nature of the elongated epidermal cells of the holdfast seems to indicate that it is secretory in nature as described by Moens (1956). Further histochemical studies should assist in getting more complete information on the development of the holdfast.

LITERATURE CITED

DARWIN, C., 1875. On the Movements and Habits of Climbing Plants. John Murray, London.

JOHANSEN, D. A., 1940. Plant Microtechnique. McGraw Hill Book Co. Inc., New York.

LAWRENCE, G. H. M., 1960. Taxonomy of Vascular Plants. Macmillan Co., New York.

METCALFE, C. R., and CHALK, L., 1957. Anatomy of the Dicotyledons. Oxford at the Clarendon Press.

MILLINGTON, W. F., 1966. The tendril of *Parthenocissus inserta*: Determination and development. Am. J. Bot. 53: 74-81.

MOENS, P., 1956. Ontogénèse des Vrilles et différenciation des ampoules adhésives chez quelques végétaux (Ampelopsis, Bignonia, Glaziovia). La Cellule 57: 371-401.

RENDLE, A. B., 1952. The Classification of Flowering Plants. Vol. II Dicotyledons. University Press. Cambridge.

SHAH, J. J., 1960. Morphohistogenic studies in Vitaceae. I. Origin and development of the axillary buds in *Cayratia carnosa* Gagnep. Phytomorphology 10: 157-174.

———, and Y. S. DAVE., 1970. Morphohistogenic studies on tendrils of Vitaceae. Am. J. Bot. 57: 363-373.

TUCKER, S. C., and L. L. HOEFERT., 1968. Ontogeny of the tendril in *Vitis vinifera*. Am. J. Bot. 55: 1110-1119.