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The origin and development of sclereids in the leaves of Camellia Reticulata Lindl

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THE ORIGIN AND DEVELOPMENT OF SCLEREIDS IN THE LEAVES OF *CAMELLIA RETICULATA* Lindl.

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by

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INTRODUCTION

In the study of plant organs it is generally found that cells are united into coherent and more or less homogenous tissues. However, one frequently finds that some plant tissues may contain isolated cells which differ considerably from neighboring tissue elements in form, size, wall structure and contents. These cells, according to botanists, are termed idioblasts. Foster (1955) recognized three types of idioblasts: (1) tracheoid idioblasts, which resemble tracheids, but differ in size and location, (2) excretory idioblasts, such as latex cells, and (3) sclerenchymatous idioblasts.

There are two types of sclerenchyma cells (Esau, 1953). They differ not only in their structure but also in their origin. One is a fiberous cell, which is long and tapered and originates from the vascular cambial initials; the other is a sclereid which arises through secondary sclerosis of a mature parenchyma cell that originates from the apical or lateral meristem. Both are non-living at maturity and have a heavily lignified cell wall.

This study is concerned primarily with sclerenchymatous idioblasts. These idioblasts are polymorphic, and are commonly termed sclereids. The term

sclereid is derived from the Greek word skleros (meaning hard). The hardness of sclereids and sclerenchyma tissue is due to their thickened cell walls, which are for the most part lignified. Their principal function is mechanical giving strength to plant tissue organs, therefore, enabling them to withstand various environmental stresses.

This paper deals with the foliar sclereid type of sclerenchymatous idioblast. The study of sclereids raises many of the fundamental problems of botany. Some of these are: growth and development, senescence of cells, intercellular relationships, and the value of idioblastic cells in systematic taxonomy. This study is not an attempt to answer all of these problems, but it is presented in the hope that it may give some additional information toward the solution of some of these fundamental problems.

SYSTEMATICS

Camellia reticulata Lindl. (*Thea reticulata* Pierre)

Camellia is a genus of evergreen trees or shrubs containing about eight recorded species which are natives of China and Japan. The camellias belong to the family *Theaceae* and are cultivated for their showy flowers, and evergreen foliage. The genus is named after George Joseph Kamel or Camellus, a Moravian Jesuit, who traveled in Asia during the seventeenth century.

C. reticulata differs from the common *C. japonica* in many ways. The ovary is pubescent, the flower is usually larger in structure, and the leaves are elliptic-oblong (Figure 1), being 3 to 5 inches long, acuminate, dull green, and not as shiny on the upper side (Bailey, 1949) as in *C. japonica*. *C. reticulata* was first recognized as a plant different from *C. japonica* by John Lindley, and in 1827 he described it as a new species (Hume, 1946).

C. reticulata originated from China, and apparently all of the plants that are now in cultivation were derived from a single clone brought to England in 1820 by Captain Richard Raws. The species was collected by Forrest in Western Yunan, China, in the vicinity of

Tengyueh (Casamajor, 1945). The exact date of its coming to America is unknown, but by the 1830's it was growing in the greenhouses of Boston, and was exhibited for the first time in a flower show in 1836 (Hume, 1946).

C. japonica is the most common garden species encountered. The reason for this, of course, is because C. reticulata is sensitive to propagation methods. Attempts at propagating this species have invariably resulted in failure. Budding and grafting techniques have been commonly employed, but have not been successful. Recently, the use of growth regulators has overcome this problem and one finds this species increasing in quantity.

The leaf, in cross section (Figure 2), is shown to be bordered by a thick cuticular layer of epidermal cells. The younger leaves show the parenchyma cells tightly packed and not distinctly separated into typical palisade and spongy areas. As the leaf matures these parenchyma cells differentiate into a single layer of palisade parenchyma and a larger area of spongy parenchyma. The veins are typical for a dicotyledonous plant.

REVIEW OF LITERATURE

Much research has been done on the growth and development of sclereids. They have been found in leaves, stems, roots, fruits, and seeds of many angiosperm species. Sclereids are not peculiar only to angiosperms, they have also been found in bark tissues (Grillos, 1956) and leaf tissues of gymnosperms (Al-Talib and Torrey, 1961). The morphology and ontogeny of many sclereids has been studied and their taxonomic importance evaluated.

Foliar sclereids are quite common in angiosperms. They have been found in the following families: Polygalaceae, Cappardaceae, Rutaceae, Simaroulaceae, Oleaceae, Trochodendraceae, Theaceae, Hamamelidaceae, Crassulaceae, Melostomaceae, Winteraceae, etc. Much of the work on foliar sclereids has been done on dicotyledonous plants, but they also occur in monocotyledonous plants. Tomlinson (1959) described the structure and distribution of sclereids in palms.

In some cases (Foster, 1944) they are found in rather compact tissues as in the petiole of C. japonica. But most commonly these cells are found in highly lacunate tissue with their radiating arms extending into intercellular air spaces. These sclereids seem to fall into two main types of distribution; diffuse and terminal. The

diffuse type is illustrated by: Ternstroemia (Rao, 1952), Olea (Arzee, 1953 a and b), Minusops (Rao and Vaswani, 1961), Trochodendron (Foster, 1945 a and b), Drimys, Belliolum, Bubbia and Zygogynum (Bailey and Nast, 1944), Illicium (Bailey and Nast, 1948), and Manilkara (Rao, 1960), in which there is no consistant relationship with the veins or veinlets. They are usually found occuring singly or clustered in the mesophyll. Some may have an apparent terminal position as Ternstroemia (Rao, 1952), but this is due to contact by the vigorous growth and development near the veinlet. The terminal type is illustrated by: Boronella (Foster, 1955 a), Mouriria (Foster, 1946 and 1947), Linociera (Rao, 1950 and 1957), Memecylon (Rao, 1954) and Nicbuhria (Rao, 1958), in which the sclereids are in contact with the vein endings. Other plants show both types of distribution in the same leaf as shown by Diospyros (Rao, 1951 b). These two types of distribution raise the problem of ontogeny of sclereids. In certain species of angiosperms the sclereids originate from initials which are located at the termination of the veins, thus giving rise to terminal sclereids. Diffuse sclereids seem to develop from cells in the parenchyma of the leaf and are usually unpredictable in their distribution and time of origin. Foard (1960) found that the diffuse sclereids of C. japonica are determined by their

position in the leaf.

Rao (1951) divides foliar sclereids into four main groups: (1) transformed epidermal cells, (2) transformed palisade cells, (3) transformed spongy mesophyll cells, and (4) transformed cells of any of the two or three regions of the leaf. Each of these groups is further subdivided into several types of sclereids on the basis of their general form. As previously mentioned sclereids are polymorphic and consequently the literature is rich in confusing terms applied.

The development of sclereids brings us to another phase of the problem which is often discussed in the literature. Do these cells grow symplasticly as other types of cells in the leaf, or by an "intrusive" type of growth? In some the sclereid growth is highly individualistic and uncoordinated with the growth pattern of other cells (Foster, 1945 b). In others (Foster, 1947) the origin and growth appears to be a part of the total growth pattern. Many leaves show a combination of the two growth patterns: symplastic growth in the early stages, and "intrusive" growth in the later stages where they penetrate between cells and into intercellular spaces (Foster, 1947 and Arzee, 1953 b). In the later case, where there are two stages of growth, symplastic growth is accepted by most botanists as the first stage in the development of

sclereids, but it is unreasonable to apply symplastic growth to the second stage in sclereid development. The second stage of growth is not clearly understood and is one of the unsolved problems in the development of these cells.

The length of time the protoplast lives varies with the species. The cytoplasm in young sclereids usually becomes highly vacuolated and may contain "plastids" (Foster, 1945 b). According to many investigators, the sclereid protoplast usually dies when the cell becomes fully developed and following this the cell cavity becomes impregnated with resins and other materials.

MATERIALS AND METHODS

C. reticulata leaves were collected from a local nursery. Leaf collections were made on two different occasions. Mature and older leaves were collected July 12, 1961. These leaves were then sectioned into smaller pieces which allowed for better penetration of killing and fixing solutions and were also more suitable for proper sectioning. The sections were taken from three different areas of the leaf: near the tip, the middle of the leaf, and near the base. These larger sections were immediately killed and fixed in Randolph's modified Navashin's formula (Johansen, 1940). The sections were aspirated to allow for better penetration of the killing fluid. After fixation for 24 hours the sections were then washed three times in 70 per cent alcohol and were then allowed to remain in this percentage of alcohol overnight. These sections were then dehydrated in 10, 20, 35, 55, and 75 per cent tertiary butyl alcohol sequence. The sections were then put into pure tertiary butyl alcohol and changed three times, the last being allowed to remain overnight.

Imbedding in paraffin was initiated by first transferring the sections into equal solutions of tertiary butyl alcohol and paraffin oil, and allowed to remain overnight. The leaf sections were then transferred to

paraffin and allowed to remain in an over overnight at 37° C. This was done to evaporate most of the tertiary butyl alcohol and to allow for paraffin infiltration. After several changes of paraffin the sections were then embedded in 56° - 58° C. Fisher Tissuemat.

The embedded sections were then trimmed and mounted on wood blocks with paraffin, and then sectioned with a rotary microtome, using a microtome blade. Razor blades proved to be too fragile for the sectioning. The sections were cut at 12 to 18 in thickness. For better sectioning the microtome blade and paraffin blocks were occasionally cooled with ice cubes.

Haupt's adhesive (Johansen, 1940) was used to mount the sections on the slides. The ribbons were flattened on a warming table and then dried overnight in an oven kept at 37° C. The mounted sections were then stained progressively in safranin and fast green, using the schedule in Johansen (1940), with some modifications. The stained sections were then mounted in Canada Balsam.

Attempts were made to obtain cleared leaf sections, using the method described by Foster (1955 b), but results were not successful.

Drawings were made with the aid of a camera lucida, and are reproduced at a magnification of approximately 450x. Diagrammatic sketches are included to illustrate the distribution of sclereids, and the normal growth pattern of a typical sclereid cell.

OBSERVATIONS

STRUCTURE OF MATURE SCLEREIDS

The sclereids in C. reticulata (Figure 3) are thick-walled at maturity and irregular in shape in contrast to other cells in the leaf. These polymorphic cells with branches radiating in various planes from the main or central "body" are found to measure up to 60 along the longest axis. Those below the midvein and along the margin are found oriented with their long axis corresponding to the long axis of the leaf. Those that are in the leaf blade often occur with the long axis at right angles to the long axis of the leaf. Many of these cells contain short protuberances on their walls which are termed "spicules" (Figure 14 and 19). The thickness of the secondary wall is found to vary with the age of the cell (Figure 4-10). In mature sclereids the cell cavities are reduced to narrow channels due to the thickness of the secondary walls (Figure 21). These secondary walls show prominent pits which are simple in structure (Figure 14). In older sclereids, as successive layers of secondary walls are deposited, many of the pits are arched over and a few functional pits are evident. The pits presumably allow the protoplast of the sclereid to be in protoplasmic contact with the other cells of the leaf. The exact

relationship of these pits to adjacent mesophyll cells was not determined.

Secondary walls appear to be concentrically lamellated in ordinary light (Figures 19 and 21). This condition is a result of successive deposition of the secondary walls and may be the result of alternation of isotropic layers of lignin with those composed of cellulose (Bailey and Kerr, 1935). The deposition of the heavily lignified secondary walls is comparatively uniform (Figure 19). The nucleus is in the central "body" of the cell and assumes an oval or crescent shape.

In general these sclereids conform to the type called "astrosclereids" (star-sclereids), cells that are ramified to varying degrees.

DISTRIBUTION OF SCLEREIDS

Sclereids in C. reticulata are distributed throughout the leaf (Figure 2). They first appear in the region of the midvein and near the margins (Figures 11-15 and 22-25). There is a heavy concentration in the mesophyll just below the midvein and in the mesophyll of the leaf margins. All sclereids are found in the parenchyma of the spongy mesophyll, with radiating arms that extend into the palisade parenchyma. None appear to penetrate through the epidermis.

None of the sclereids are in contact with the vein endings, as noted in other dicotyledonous plants. All occur as isolated or clustered idioblasts unrelated to the veinlets or vein endings. There is no evidence to indicate their distribution is determined by their position in the leaf.

ORIGIN AND DEVELOPMENT OF SCLEREIDS

Sclereids originate from apparently normal parenchyma cells in the spongy mesophyll of the leaf. Their radiating arms may be found in the palisade parenchyma, but none originate here as reported by Rao and Vaswani (1961) in Minusops. The sclereid initials develop during the final phase of the enlargement of the leaf, and can be distinguished from other adjacent parenchyma cells by having a larger nucleus, and later by their larger size and thinner walls (Figures 11, 16 and 22). The young developing sclereid initial grows first by symplastic growth, which is normal for all types of cells, and then followed by "intrusive" growth, which permits radiating arms to penetrate between the middle lamellae of the adjacent cells and also into the intercellular air spaces (Figures 4-10 and 11-14). Although the intercellular air spaces are beginning to form at this stage of development there is no evidence to indicate that the position, direction, number, size and shape of the radiating arms is determined by the air spaces. When the sclereid reaches

its full size the internal area is a highly vacuolated unit with little cellular content (Figures 11, 16 and 22). After the termination of its enlargement and intercellular branching it begins to deposit layers of secondary walls, one on another toward the center of the cell. The secondary walls then push the protoplast towards the center of the cell, where a smaller cell cavity is found. The nucleus changes its shape during the time the cell is developing. It progresses from a spherical (Figure 11) to a crescent shaped (Figure 21) unit. In mature cells (Figure 21) the nucleus remains distinguishable. The presence of the nucleus indicates that the protoplast does not die at maturity as reported in other sclereids, but remains living throughout the life of the leaf.

In summary the fully developed sclereid shows a well defined secondary wall, a relatively small cell cavity, in which is found the protoplast.

DISCUSSION

The sclereids in C. reticulata originate at random and develop from parenchyma cells in the mesophyll layer of the leaf. Why is it that a normal parenchyma cell undergoes a type of secondary differentation and ultimately develops into a sclereid? Is the sclereid a result of some physiological difference in certain parenchyma cells, is there a genetic difference, or is it determined by the position of the cells in the leaf? These problems still need, of course, further investigation, particularly from a physiological standpoint.

Sclereids begin their early development at approximately the same time that the leaf is in its final stages of enlargement. The formation of intercellular air spaces during this enlargement undoubtedly facilitates the expansion of the sclereid initial's primary wall. The sclereid initials are not limited to the intercellular air spaces, but grow between neighboring cells (Figures 17-19). Foster (1944) found in the leaf of C. japonica that these cells begin their growth during the final phase of enlargement of the leaf and occur in rather compact tissues.

It is generally agreed that most sclereids undergo two phases of growth. The first phase is a symplastic growth and is a pattern which is accepted by most

investigators. The second phase involves the penetration of the radiating arms into air spaces and between the middle lamellae of the adjoining cells. There is no total agreement on this phase of growth. Foster (1947) describes it as "apical growth", Kuster (1925) adopts the concept of "gliding growth", whereas, Sinnot and Block (1943), and Block (1944) favor "intrusive growth". There is some evidence to support all these theories, also evidence contrary to the fact. The occurrence of spicules does not support the "intrusive growth" theory, and "gliding growth" is criticized as not taking into account the protoplasmic connections. It is easily demonstrated that sclereids grow between adjacent cells but the mechanics of how they grow is still unknown and this is the reason for so many conflicting ideas. It can be best summed up by implying that this type of a cell is a "highly plastic entity".

There is no indication of the sclereid initials or mature sclereids having any contact with vein endings, as noted in the following genera, Boronella, Boronia, Mouriria, etc. There is some indication that sclereids may be determined by position in the leaf (Foard, 1960), when one notes the regular occurrence near the midvein and also along the margins. This does not explain the random distribution throughout the blade of the leaf. The evidence seems to indicate that sclereids develop

independently of one another and the remaining cells in the leaf (Figure 12).

The protoplast in the developing sclereid is characterized by being highly vacuolated and containing a large nucleus, which remains intact throughout the life of the cell. Grillos (1956) found that the protoplast of of sclereids in Pseudotsuga disappears at maturity. There is no evidence of a multinucleate stage, as noted by Sterling (1947) in the work on the shoot of Pseudotsuga. There is no indication of discoid bodies which Foster (1945 b) found and interpreted as "plastids".

The exact reason why parenchyma cells develop into sclereids is still unsolved. Little, if anything, has been done on the biochemical aspects of this type of development. Probably a great deal would be learned if botanists would employ some histo-chemical techniques to the study of the problem.

SUMMARY

The young leaf of C. reticulata shows sclereids in the mesophyll below the midvein and near the margins. These cells are independent idioblasts showing no relationship with the vein endings. Their distribution through the blade of the mature leaf is at random.

Sclereids begin their growth with the final stages of enlargement of the leaf. They originate from parenchyma cells which enlarge rapidly, first by a symplastic phase and then by an "intrusine" phase. During this enlargement they ramify into the intercellular air spaces and middle lamellae of the adjacent mesaphyll cells. When growth is near completion the protoplast actively deposits secondary wall layers on the primary wall and these are traversed by simple pits. The nucleus goes from a spherical to an oval or crescent shaped structure and remains in the center of the cell. The protoplast remains living throughout the life of the leaf.

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FIGURES AND DESCRIPTIONS

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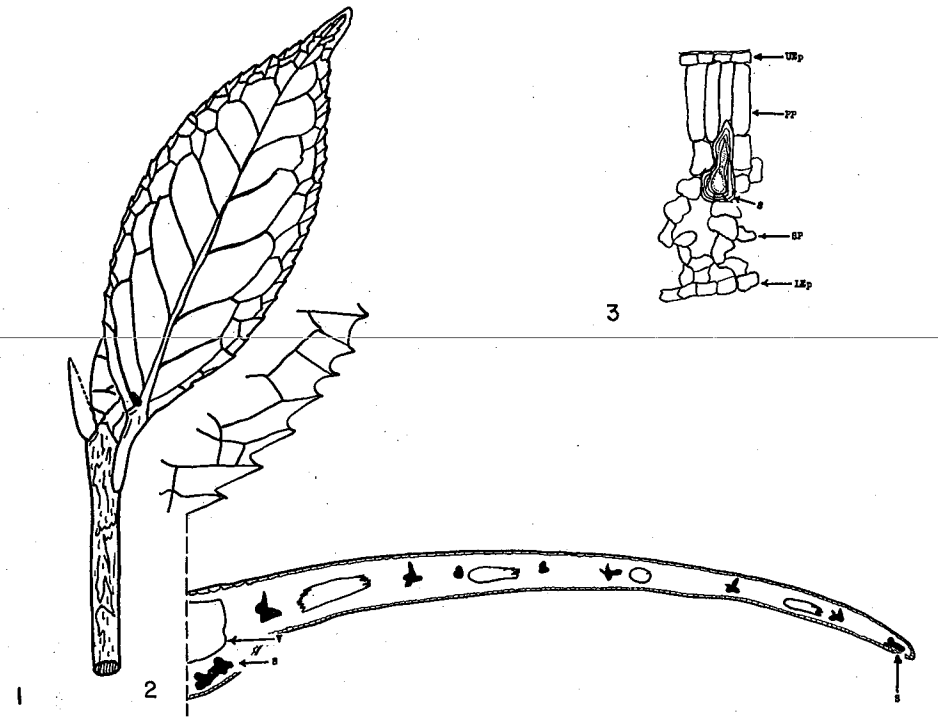
PLATES I-IV

EXPLANATION OF SYMBOLS USED IN LABELING THE ILLUSTRATIONS

C	--	cytoplasm
Cu	--	cuticle
LEp	--	lower epidermis
Mv	--	midvein
N	--	nucleus
P	--	pit
PP	--	palisade parenchym
PCW	--	primary cell wall
S	--	sclereid
SI	--	sclereid initial
Sp	--	spicule
SP	--	spongy parenchyma
UEp	--	upper epidermis
V	--	vein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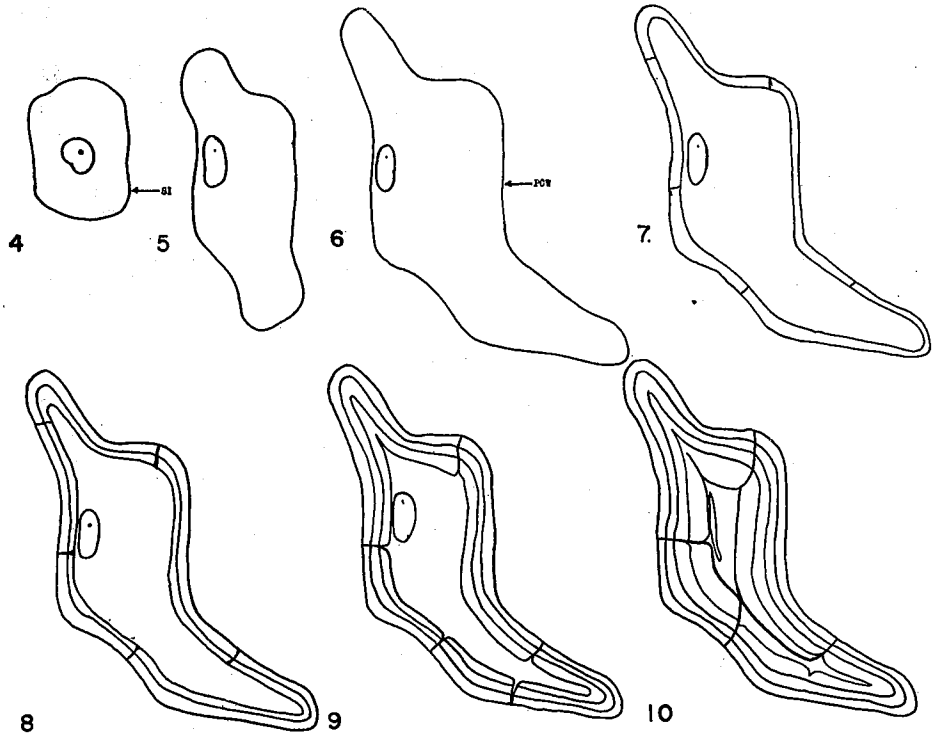
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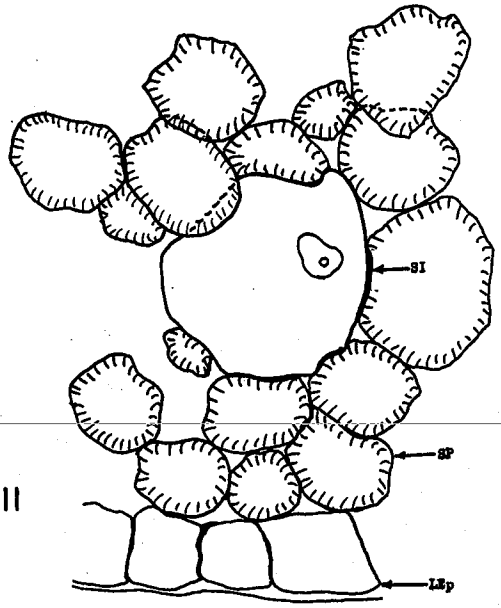

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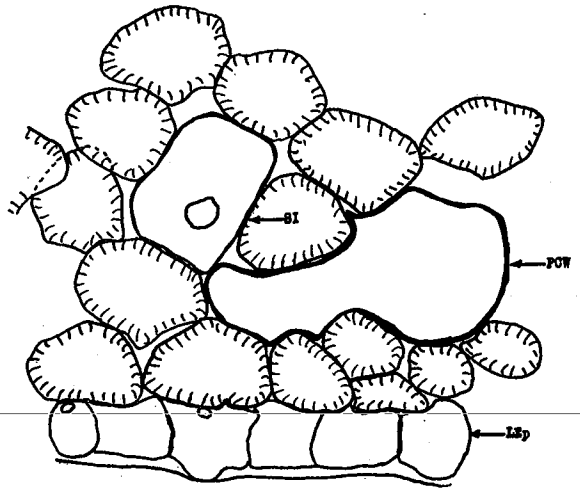

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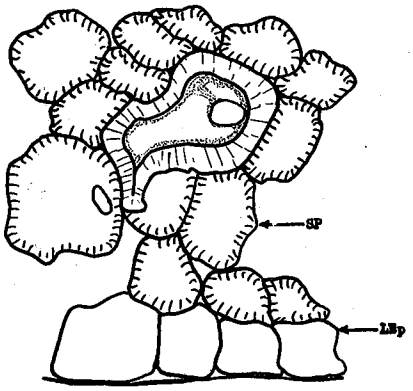

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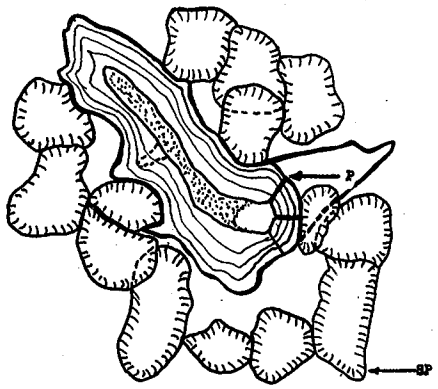

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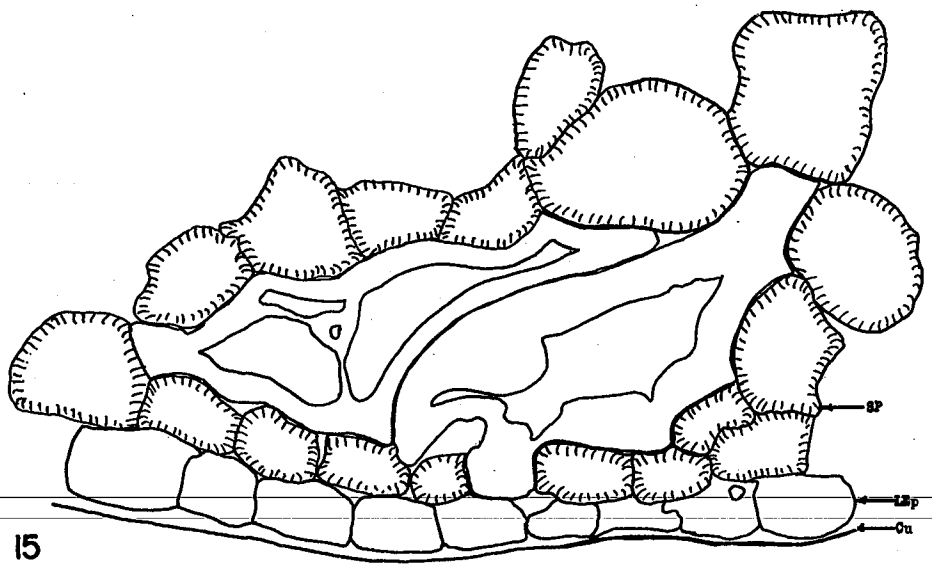

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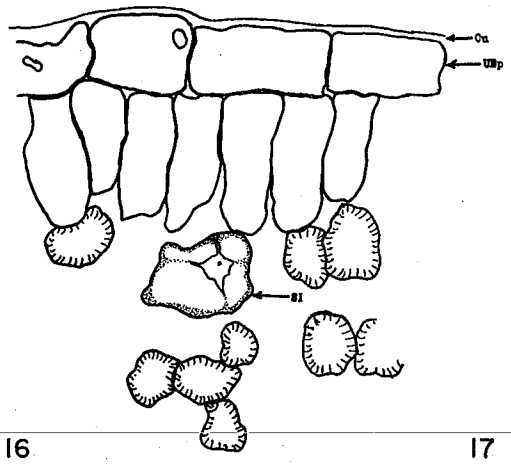

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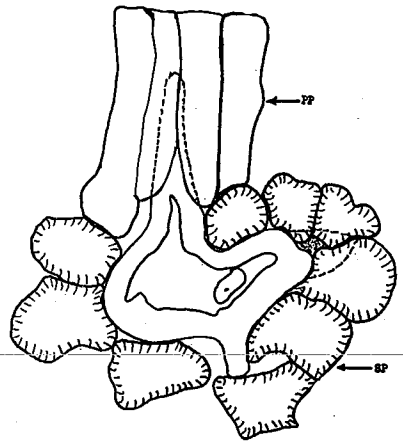

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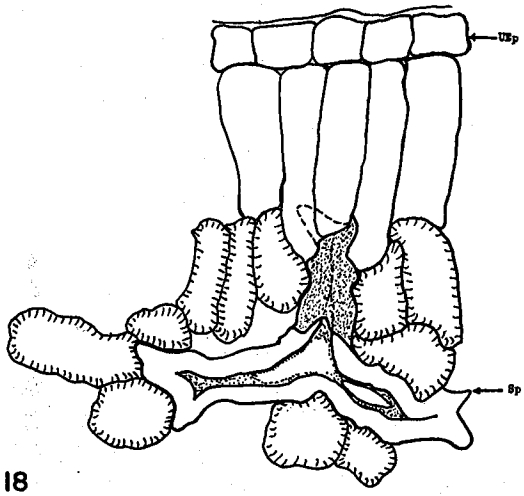

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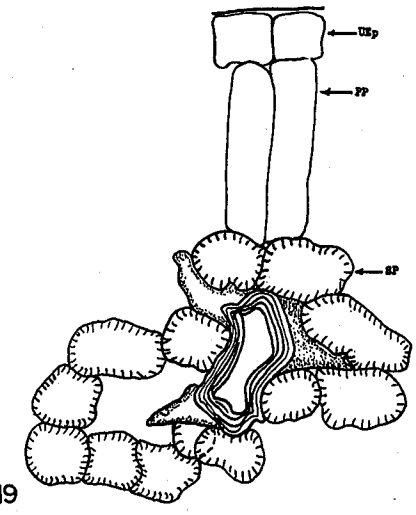

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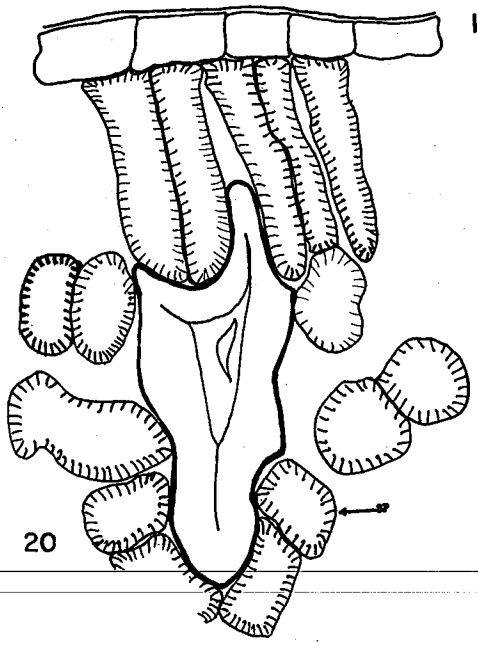

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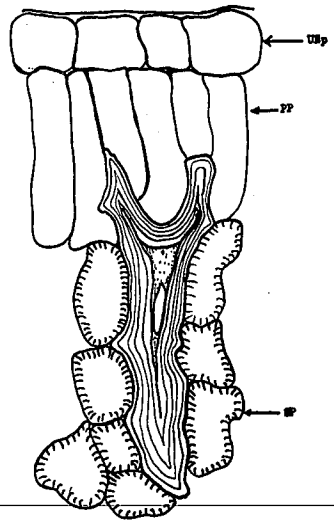

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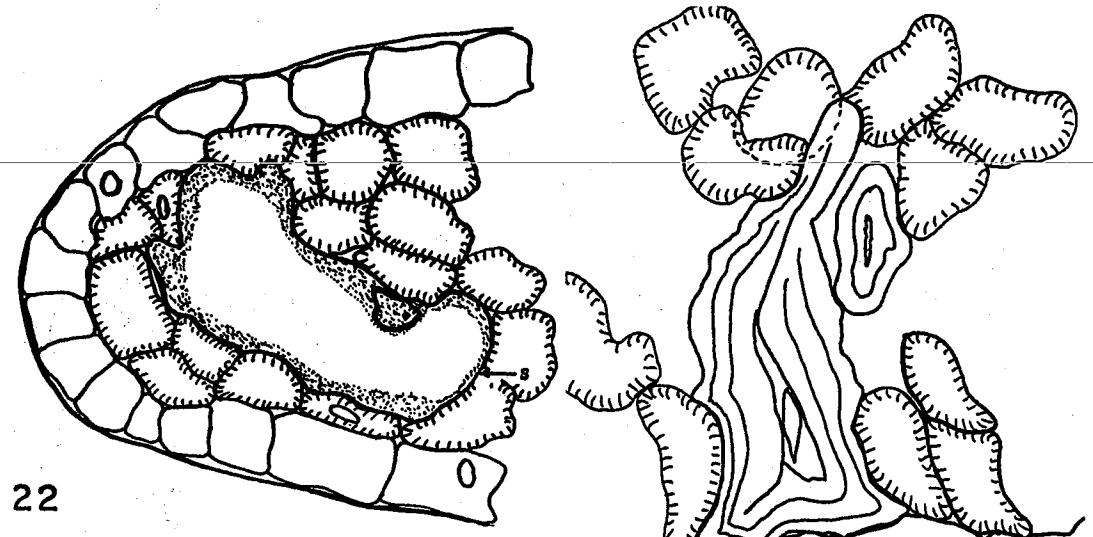

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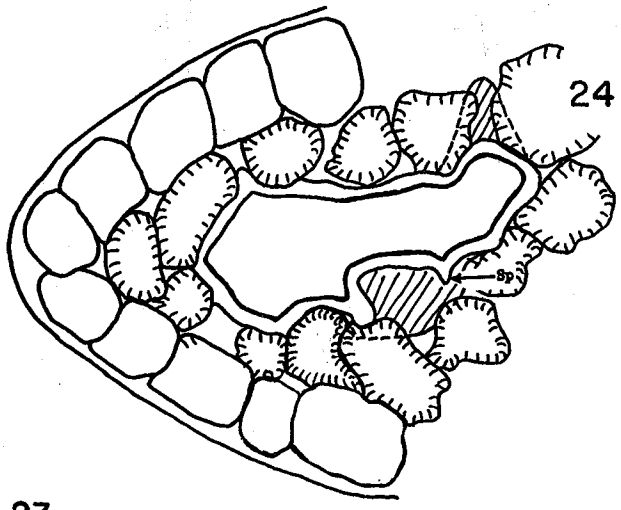

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