PLANT ANATOMY

A. FAHN

Professor of Botany
The Hebrew University, Jerusalem, Israel

Translated from the Hebrew by SYBIL BROIDO-ALTMAN

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CHAPTER 7

XYLEM

THE vascular system of the sporophytes of the higher plants consists of *xylem*, the main function of which is the transport of water and solutes, and *phloem* which mainly transports the products of photosynthesis.

On the basis of its physiological and phylogenetic importance, the vascular system, and especially the xylem, has been used for the classification of a large group of plants. The term *vascular plants* was first used in 1917 by Jeffrey. Recently the term *Tracheophyta* has been introduced to cover this group of plants which comprises the Pteridophyta and Spermatophyta. The term Tracheophyta has been derived from the xylem, and not the phloem, because of the firm and enduring structure of the tracheary elements. These elements have thick, hard walls and so can be distinguished more easily than the phloem elements. Also the xylem is more readily preserved in fossils and so can be identified more easily.

Xylem is a complex tissue as it consists of several types of cells. The most important cells are the *tracheary elements* which are the non-living cells that are principally concerned with the transport of water and which also, to a certain degree, have a supporting function. Fibres are present in the xylem where they are mainly concerned with the strengthening of the plant body. Sclereids also may be sometimes present. Parenchyma cells which have storage and other functions also occur in the xylem. The xylem of some plants contains laticifers (see Chapter 9).

The xylem and phloem elongates in developing organs by the continual differentiation of new elements produced by the procambium, which itself is continuously produced by the apical promeristem. The xylem produced by the procambium in the primary body is called the *primary xylem*. In many plants, after the completion of the formation of the primary body, secondary tissues are developed. The xylem that is produced as a result of the activity of the vascular cambium is called the *secondary xylem*.

In the primary xylem the elements that are completed early, i.e. the *protoxylem*, are distinguished from those completed later, i.e. the *metaxylem*.

Tracheary elements

Two basic types of tracheary elements are distinguished—*tracheids* and *vessel members*. The term tracheid was introduced in 1863 by Sanio who discussed the similarity and differences between this element and the vessel member. Since then much work has been devoted to the investigation of the structure, shape, function, ontogeny and phylogeny of these elements.

The main difference between tracheids and vessel members is that the former are not perforated while the end walls of the latter are perforated (Fig. 45). A vessel, which is also termed a *trachea*, is built of numerous vessel members that are joined one to the other by their end walls. Vessels are terminated by a vessel member of which the proximal end wall is perforated, whereas the distal end wall is not, i.e. the distal parts of a vessel is tracheid-like.

STRUCTURE AND SHAPE OF THE SECONDARY WALL OF TRACHEARY ELEMENTS

In a radial longitudinal section of vascular bundles it can be seen that the tracheary elements differ one from the other in the shape and structure of the secondary wall. In many plants the secondary wall thickening of the first-formed xylem (protoxylem) is annular or helical (Fig. 43, nos. 7–9; Fig. 44, no. 1). The helical thickening may be single, or more than one helix may be present in a single element. The rings or helices may be arranged in a loose or a dense manner. From an ontogenetic viewpoint, the annular elements precede the helical elements. In later-formed tracheary elements the helical bands become joined in certain areas giving rise to a ladder-like type thickening; such thickening is termed *scalariform thickening* (Fig. 43, no. 10). In tracheary elements formed at a still later ontogenetic stage the wall thickening is in the form of a network, i.e. *reticulate thickening* (Fig. 43, no. 11). When the openings in the secondary wall of such a network are elongated in a direction perpendicular to the longitudinal axis of the element, the thickening is termed *scalariform-reticulate*. In the ontogenetically most advanced elements, the secondary cell wall is interrupted only at the pits; such elements are termed *pitted elements* (Fig. 44, no. 2). Pitted elements are characteristic of the late primary and of the secondary xylem. Not all the above types are always found in a single plant. On the other hand, intermediate types not mentioned above can be found, as well as combinations of more than one form of thickening which may occur in a single element. The annular and helical wall thickenings may vary in thickness and certain helices are so deeply grooved on their inner surfaces as to appear double (Fig. 43, no. 6). In some cases the helical thickening is joined by a narrow strip to the primary wall (Fig. 43, nos. 5, 6).

The pits in pitted tracheary elements are bordered. The well-developed bordered pit-pairs which are usually present between two tracheary elements are termed *intervascular pits*. Between tracheary elements and fibres there may be only a few small pits or even none at all. Between tracheary

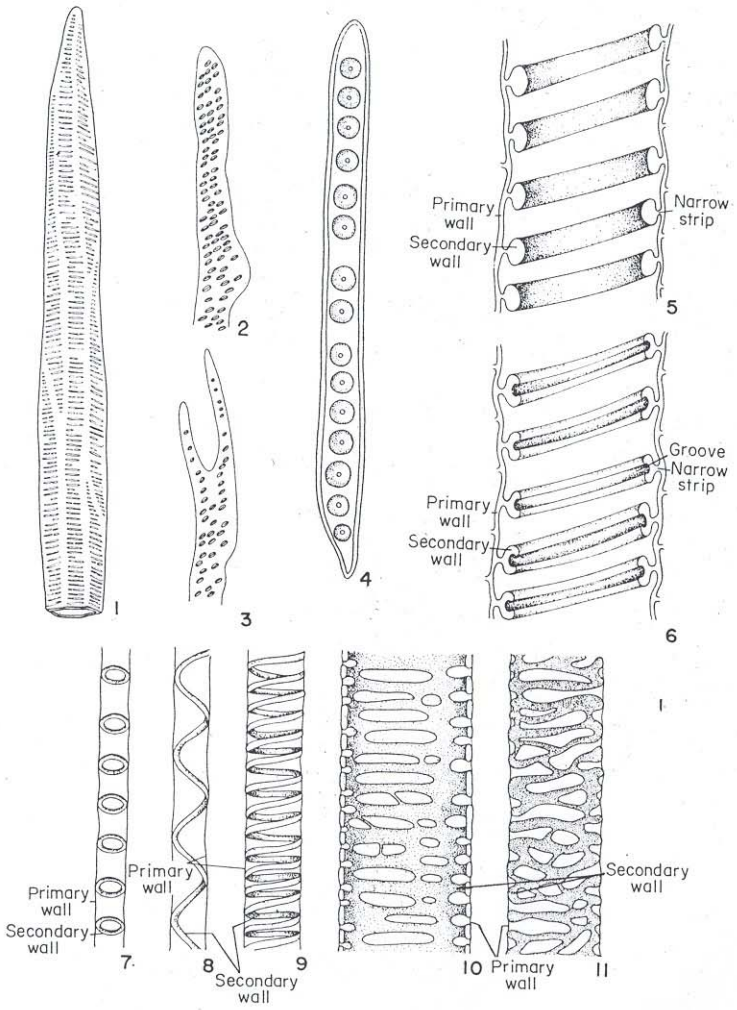

FIG. 43. 1, Tip of tracheid of *Dryopteris;* with scalariform pitting. 2 and 3, Tips of tracheids of *Kingia*. 4, Tracheid of *Pinus*. 5, Portion of a longitudinally sectioned tracheary element showing the helical wall thickenings and the strips by which they are joined to the primary wall. 6, As in no. 5, but in which the helical thickening is deeply grooved. 7–11, Different types of wall thickening in tracheary elements. 7, Annular thickening. 8, Helical thickening. 9, Dense helical thickening. 10, Scalariform thickening. 11, Reticulate thickening.

elements and parenchyma cells the pit-pairs are mostly half-bordered, i.e. bordered on the side of the tracheary element and simple on the side of the parenchyma cell.

When the bordered pits are transversely elongated and are arranged in longitudinal rows along the element, the pitting is termed *scalariform pitting* (Fig. 18, no. 2). Circular and elliptical pits are arranged in horizontal or diagonal rows. The former arrangement is called *opposite pitting* (Fig. 18, no. 4) and the latter *alternate pitting* (Fig. 18, no. 5). On the inside surface of a pitted secondary wall a helical thickening may develop (Fig. 132).

In the Ophioglossales, the Ginkgoales, the Coniferales and the Gnetales no scalariform pitted elements are found. In plants of these orders bordered pits, which are similar to those found in the secondary tracheary elements of the same plant, are found on the reticulate and helical thickenings of the primary xylem (Fig. 46, no. 10).

The following facts are known about the formation of the special wall thickenings of the tracheary elements.

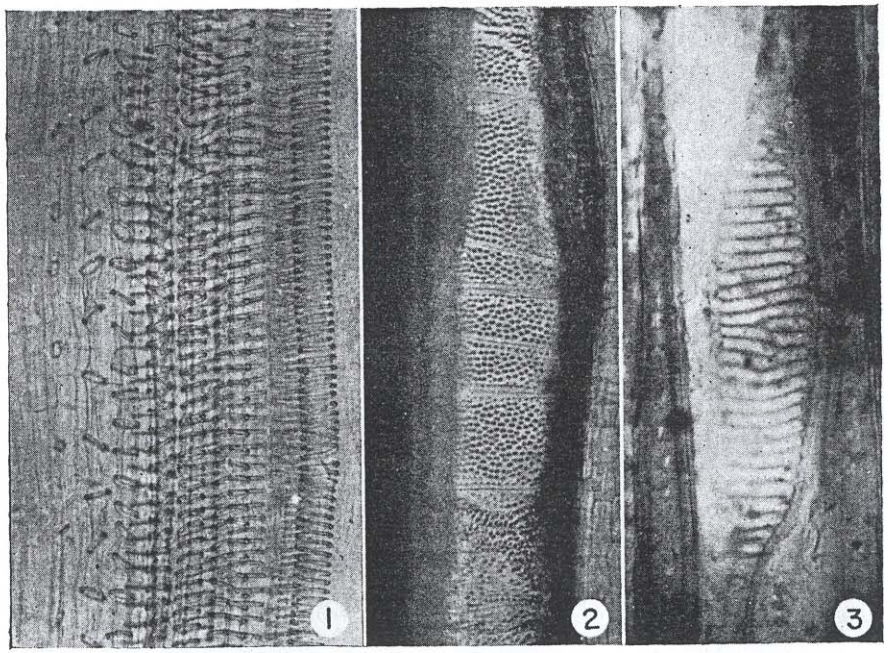

FIG. 44. 1 and 2, Micrographs of longitudinal sections of the young stem of *Cucurbita*. ×150. 1, Protoxylem elements with annular and helical thickening. 2, Pitted metaxylem vessel. 3, Micrograph of a radial longitudinal section in the secondary xylem of *Viburnum tinus* showing a scalariform perforation plate. ×470.

Crüger (1855) observed that in the positions where the thickenings of the secondary wall will develop, strips of actively streaming cytoplasm appear. Similar conclusions were reached by Barkley (1927) who believed that the position of the cytoplasmic strips is determined by the position of rows of vacuoles.

A similar phenomenon was also observed by Sinnott and Bloch (1945) who studied the development of tracheary elements from parenchyma cells during the regeneration in the vascular bundles of *Coleus*. Interesting observations were made by Majumdar (1940, 1941) who worked on the development of vessels in the protoxylem of *Heracleum*. Recently Wooding and Northcote (1964) suggested that the Golgi apparatuses are involved in the formation of the wall thickenings.

There is also evidence that the cytoplasm of the developing tracheary element lines the cell wall with suberin (Scott *et al.*, 1960).

The functional significance of the different types of wall thickenings in the tracheary elements is not clear. It is possible that the exclusive appearance of annular and spiral thickenings in elements in those organs that are still elongating has some connection with the rapid increase in length of the organ. Investigations using X-rays together with the regulation of light which altered the rate of stem elongation proved this assumption. Goodwin (1942) and Smith and Kersten (1942) saw that if stem elongation is inhibited the production of annular and spiral vessels is reduced or stopped and pitted vessels develop.

VESSELS AND THE STRUCTURE OF PERFORATION PLATES

As has been mentioned previously, two main types of tracheary elements can be distinguished—tracheids and vessel members. Tracheids are non-perforated cells in which only bordered pit-pairs are found in the areas of contact between them, while vessel members are perforated at their ends. By these perforations the vessel members become joined to form a tube-like series of cells which is termed a *vessel* or *trachea*. Vessels are limited in length and those vessel members which terminate a vessel are perforated on one end only, i.e. the terminating end is not perforated. Therefore the passage of water from vessel to vessel takes place via the pits as from tracheid to tracheid. It is difficult to measure the length of vessels but this was done successfully by Handley in 1936 who made use of the fact that, although water and solution pass through the pits, gas does not. Handley forced coal gas into one end of a cut branch and attempted to light it at the other end. From such experiments he came to the conclusion that the length of the vessels in *Acer* is about 60 cm and in *Fraxinus* about 3 m.

The vessel members are usually perforated on the end walls but sometimes the perforations are formed on the side walls. Those parts of the cell wall that bear perforations are called *perforation plates*. The perforation plate may contain one large perforation and then it is termed a *simple perforation plate* (Fig. 45, nos. 4–6), or it may contain numerous perforations. In the latter case there are several possible ways in which

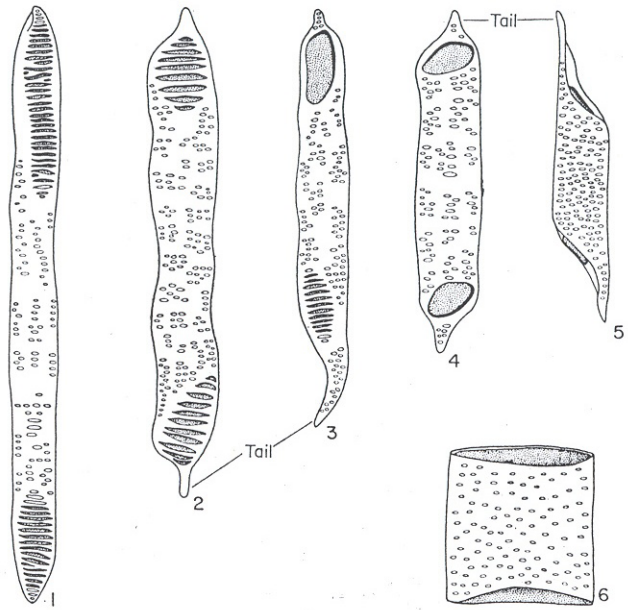

FIG. 45. Dicotyledonous vessel members. 1 and 2, Vessel members in which the perforation plates at both ends are scalariform. 3, Vessel member with one scalariform and one simple perforation plate. 4–6, Vessel members with simple perforation plates. "Tails", the narrow elongated tips of the vessel members, can be seen in nos. 2–5. (Adapted from Bailey.)

the perforations can be arranged. When the perforations are elongated and are arranged in a parallel series the plate is termed a *scalariform perforation plate* (Fig. 44, no. 3; Fig. 45, nos. 1, 2), when in a reticulate manner, *reticulate perforation plate* (Fig. 46, nos. 2, 4) and when the perforations are almost circular the plate is termed a *foraminate perforation plate* (Fig. 46, no. 11).

The scalariform perforation plates may sometimes be very long and then they contain hundreds of perforations. In such cases the end wall bearing the plate is very long and oblique so that it is sometimes difficult to decide whether it is a vessel member or a tracheid. The identity of these elements can be established by passing a carbon suspension through sectioned portions of branches. The suspended particles can pass only

through perforations as the pit membrane prevents their passage through the pits. However, sometimes even the above method is not reliable and a further method in which very fine longitudinal sections of the perforation plate are cut, is used in order to discover if the primary wall is present or

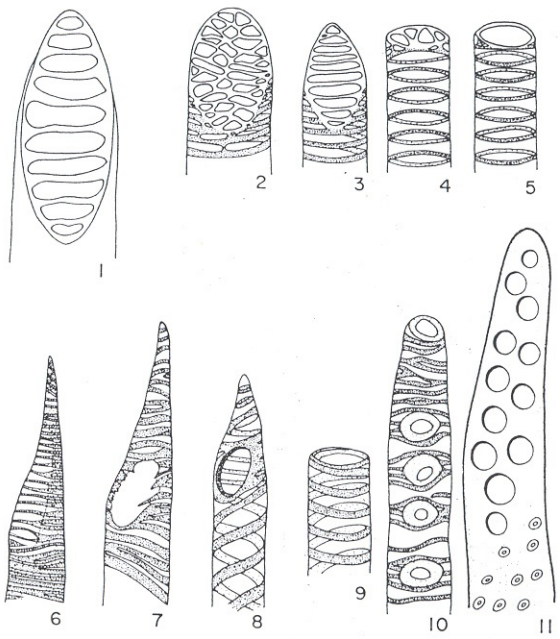

FIG. 46. 1–5, Perforation plates of vessel members in the primary xylem of monocotyledons. 1, Scalariform perforation plate from the stem of *Phoenix dactylifera*. ×70. 2, Reticulate perforation plate from the root of *Hymenocallis caribaea*. ×200. 3–5, Vessel members from the stem of *Rhoeo discolor*. ×150. 3, Scalariform perforation plate of a helically-thickened vessel member. 4, Reticulate perforation plate of an annularly-thickened vessel member. 5, Simple perforation plate. 6–9, Ends of vessel members with helical thickening from dicotyledonous primary xylem. 6, Scalariform perforation plate. 7, Transitional form between a scalariform and simple perforation plate. 8 and 9, Simple perforation plates. 10, Tracheid of *Gnetum* with helical thickening and circular bordered pits. 11, Vessel member end of *Ephedra* with a foraminate perforation plate. (Nos. 1–5, adapted from Cheadle, 1953; nos. 6–10, adapted from Bailey, 1944.)

not. This method also involves technical difficulties. It may be that some of the gaps in the secondary wall are perforations and some are pits. It has been suggested that such intermediate forms between typical tracheids and typical vessels should be termed *vessel-tracheids* (Fahn, 1953) or *vessel member-tracheids* by analogy with fibre-tracheids, which are intermediate between fibres and tracheids.

In many dicotyledonous species the middle portion of the vessel members of the secondary xylem widens during ontogenetic development while the tips remain narrow and elongated. These tips are not perforated and they appear as projections that overlap the walls of the neighbouring vessel members; these tips have been termed *tails* (Chalk and Chattaway, 1934, 1935). The perforations are present at the end of the widened part of the element, i.e. near the base of the tails (Fig. 45, nos. 2–5).

DEVELOPMENT OF VESSELS

Vessels develop from meristematic cells — procambial cells in the primary xylem and cambial cells in the secondary xylem. The vessel members may or may not elongate prior to the thickening of the wall but they usually widen in this stage of development.

Much attention has been paid by workers studying the ontogeny of vessels to the end walls in which the perforations develop. Different opinions exist as to how the perforations develop. According to Esau and Hewitt (1940), who worked on herbaceous plants in which the vessel members had simple perforation plates, layers of the secondary wall are deposited on the primary wall in the pattern specific for each type of vessel after the vessel members have reached their maximum size. Those parts of the primary wall in the position where the perforation will develop do not become covered with secondary wall substance, but they become thicker relative to the other area of the primary wall of the element (Fig. 47, nos. 1–3). This thickening apparently is not the result of the addition of material to the wall but the result of the swelling of intercellular substance. After the secondary walls are completely developed and lignified the swollen parts of the primary wall and middle lamella slowly disintegrate. This process is apparently brought about by the protoplast which itself later dies and disintegrates (Fig. 47, no. 4).

According to Priestley *et al.* (1935), who investigated the development of the vessels in trees, the production of the perforation in the end wall is a sudden process and no intermediate stages can be found. Apparently, while the walls are still very thin, the end walls contract suddenly, and so the rim or rims around the perforations are formed (Fig. 47, no. 5). Often a stretched pectic membrane remains in the position of the perforation. By means of plasmolysis the above workers were able to show that each vessel member has a separate protoplast during all stages of the thickening and lignification of the wall.

In ring-porous and sometimes in diffuse-porous wood, in which the vessels are wide, as the vessel grows in width the cells neighbouring it may become separated one from the other. In this way the vessel is brought into contact with new cells (Fig. 47, nos. 6, 7). In many cases it is possible to

observe that where the position of the above separating cells is shifted relative to the widening vessel, the cells retain their original attachments, or at least partially so, in those positions where there are pits. This is possible by the extension of the cell wall to form bridge-like connections in the region of the pits (Fig. 47, no. 8). According to Priestley *et al.* (1935) this

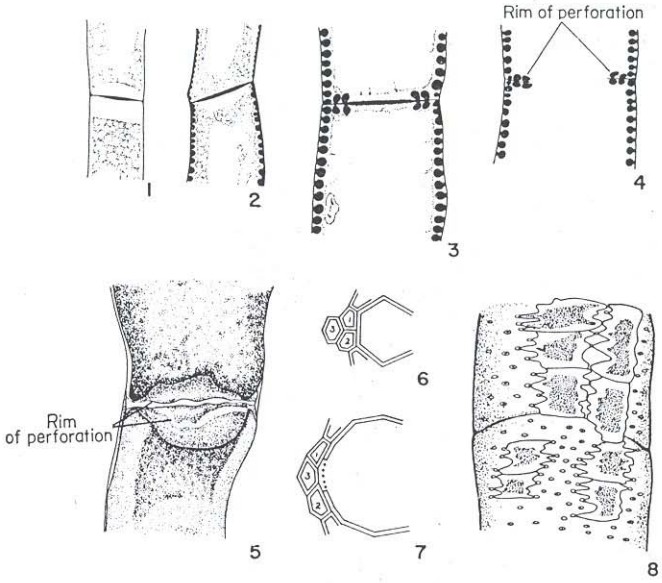

FIG. 47. 1–4, Development of a perforation plate in vessel members of *Apium graveolens*, after Esau, 1936. The development of helical secondary thickening on the side walls and the presence of the primary end wall can be seen in nos. 1–3. The end wall has disappeared in no. 4. 5, End portions of two adjacent vessel members of *Fraxinus* in which it is possible to distinguish the perforation rim and the two protoplasts that have separated from one another. ×125. 6 and 7, Diagrams of cross-sections of a vessel and neighbouring cells showing how the vessel, during enlargement, comes into contact with new cells. Neighbouring cells indicated by numerals. 8, Drawing of portion of a vessel of *Ulmus* in surface view, showing how the cells around the vessel tear away from each other as a result of the widening of the vessel. The neighbouring cells retain their original attachments to the vessels where there are pits, resulting in the formation of bridge-like extensions. ×95. (Nos. 5–8, adapted from Priestley *et al.*, 1935.)

phenomenon is apparently made possible because of the greater plasticity of the pits themselves or their margins. These workers state that in ring-porous wood the cells surrounding the vessels differentiate prior to the vessels or, at latest, simultaneously with them and therefore the above separation takes place. In diffuse-porous wood the walls of the cells next to the vessel become thickened and lignified somewhat later than those of the vessel members.

PHYLOGENETIC DEVELOPMENT OF TRACHEARY ELEMENTS

The xylem holds an important position in the study of plant tissues as the structure of its elements is of extreme importance in taxonomy and phylogeny. More attention has been paid to the phylogenetic development of xylem than to any other tissue. The structure of the tracheary elements has been studied in special detail. The research has been aided by statistical methods which emphasize the differences in structure and shape of the tracheary elements and which have explained their phylogenetic significance.

It has been obvious for a long time that the tracheid is a more primitive element than the vessel member. The tracheid is the only tracheary element found among Pteridospermae, in fossil Spermatophyta, in most of the lowest vascular plants of today, and in nearly all the Gymnospermae. It is commonly accepted that vessel members have developed from tracheids. Vessel members occur in the following diverse groups of plants: in the most advanced gymnosperms, the Gnetales; in dicotyledons except for the lowermost taxonomic groups; in monocotyledons; in the fern, *Pteridium;* in certain species of *Selaginella;* and in *Equisetum* (Bierhorst, 1958). From the above it can be assumed that vessels developed independently, by parallel evolution, in each of these groups.

ORIGIN AND PHYLOGENETIC DEVELOPMENT OF VESSEL MEMBERS IN ANGIOSPERMS

In order to understand the problems of plant phylogeny, fundamental methods of logic have been used. Frost (1930 a, b; 1931) clearly defined some of these fundamental logical assumptions while trying to establish the origin of the vessels in the dicotyledons. The following are the principal assumptions used by Frost.

1. *The association method.* This method states that if it is possible to determine which of two structures is the more primitive, and if it is assumed that the two structures have a direct genetical relationship, it will be possible to conclude that the primitive condition of the more advanced structure will be similar to the general condition of the primitive structure. If there is not much similarity then the assumption of direct genetical relationship is not correct or the elements in question are, apparently, so far separated in the scale of evolution that the primitive form of the advanced element has been lost. Therefore, with reference to tracheary elements, if it is assumed that the tracheids are more primitive than the vessel members and that the two elements have a direct genetical relationship, then it must be concluded that the most primitive vessel members will be those that are most similar to tracheids.

2. *The correlation method.* By this method it is assumed that in a certain homogeneous tissue, as, for instance, the secondary xylem, there will

exist a statistically significant correlation between the degrees of specialization of the main characteristics of a structure in a large random sample (many species), i.e. the various features have undergone evolutionary changes simultaneously. Therefore, features occurring together with those features that are defined as being primitive, by the association method, are themselves primitive, and those that occur together with features defined as being advanced, are advanced. It is necessary to bear in mind that such correlations express only the general trends of development and that exceptions exist. The development of some features may be delayed and of others advanced. The investigation of these exceptions can indicate the lines of secondary specialization which only become clear after the principal lines of development have been determined. In relation to the vessel members, if great length is a primitive feature (as is derived by the association method) then all other features that are found in correlation with great length are also primitive features.

3. *The sequence method.* This method deals with the reconstruction of the evolutionary variability on the basis of the variation, as seen in living forms. These variations can be seen ontogenetically or by the comparison of different plants belonging to a single taxonomical group. The contribution of this method to the problem of the origin of vessels has been the determination of the origin of vessel members from tracheids with scalariform pitting. Typical tracheids of this type appear only in the secondary wood of those dicotyledonous genera that have no vessels, e.g. genera of the Winteraceae, Monimiaceae, Chloranthaceae and Tetracentraceae, but are completely absent from the secondary xylem of angiosperms that contain vessels (Bailey, 1944). In some trees and large shrubs of various primitive dicotyledonous families, the vessel members of the secondary xylem are similar in size, angular cross-section, pitting and thin secondary walls to tracheids with scalariform pitting. It is important to mention that the scalariform pitted tracheids have served as the origin not only of vessel members but also of tracheids with circular bordered pits and apparently also, indirectly, of fibre-tracheids and libriform fibres (Tippo, 1946; Bailey, 1936, 1953). The complete or almost complete absence of primitive tracheids with scalariform pitting in the Angiospermae is related to their development, in the process of phylogeny, into vessel members or into tracheids with a more advanced form of pitting.

The following structural features of the angiosperm tracheary elements are those that are used as a basis for the study of their evolution.

1. *The length of the element.* The tracheids are long cells whose average length reaches 4·35 mm in *Trochodendron*, a vessel-less dicotyledon (Bailey, 1944). Their average length as calculated from many hundreds of measurements made in monocotyledons is 5·07 mm (Cheadle, 1943a). In monocotyledons, according to Cheadle, vessels can be divided into four groups, according to their degree of specialization. The average lengths of the vessel members in these four groups are 3·96 mm, 2·58 mm, 1·47 mm and 0·76 mm. As the vessel members are shorter than the tracheids the shorter the vessel member, the more advanced it is considered to be.

2. *The diameter of the element.* The diameter of the tracheid is smaller than that of the vessel member.

3. *The thickness of the wall.* The wall of a typical tracheid is thin and is of equal thickness over the entire circumference. This feature is also seen in primitive vessel members.

4. *The perforation plates.* Those scalariform perforation plates that are long, oblique and with numerous perforations are considered the most primitive and the simple, horizontal perforation plates the most advanced.

5. *The shape of the element in cross-section.* The shape of the tracheids and the primitive vessels in cross-section is angular, while that of advanced vessel members is circular or nearly so.

6. *The type of pitting.* In the dicotyledons scalariform pitting in vessel members is considered to be primitive. The structure and arrangement of pits developed, from scalariform pitting, through intermediate forms in which scalariform pits occur together with circular or elliptical pits (Fig. 18, no. 3), to forms with only circular or elliptical pits. Of this advanced type of pitting, that in which the pits are arranged in parallel rows, i.e. opposite pitting, is more primitive than alternate pitting, in which the circular or elliptical pits are arranged along more or less helical lines (Fig. 18, nos. 4, 5). The appearance of the spiral thickenings on the inside of the secondary wall of the tracheary elements is evidence of advanced development.

The phylogenetic development of the side walls of the tracheary elements was prior to that of the perforation of the end walls.

SUMMARY OF SUGGESTED ORIGIN AND SPECIALIZATION OF VESSELS

From investigations based on the methods and facts that have been mentioned above and which have been made over the last 30 years, the present knowledge of the evolutionary development of the mono- and dicotyledonous vessel members can be summarized, after Cheadle (1953), as follows:

Dicotyledons

1. Ten woody genera are known that completely lack vessels. These genera belong to the following five families: Chloranthaceae, Winteraceae, Tetracentraceae, Trochodendraceae and Monimiaceae.

2. There are 52 out of 147 families that consist of woody plants only and that contain one or more species that have only scalariform-perforated

vessel members. The following are some of these families: Aquifoliaceae, Betulaceae, Buxaceae, Celastraceae, Magnoliaceae, Myrtaceae, Styracaceae.

3. Of 82 families that contain both woody and herbaceous species, only 7 families contain one or more species with exclusively scalariform-perforated vessel members.

4. Of the herbaceous plants, the internal structure of which has been adequately studied, only *Paeonia* of the Ranunculaceae, *Pentaphragma* of the Campanulaceae, and a few other species of three other families have exclusively scalariform-perforated vessel members. However, in these examples the perforation plate is mostly not of the very primitive type as the plate is short and has only a few perforations.

5. Of the remaining herbaceous families, in 61 families only vessel members with simple perforation plates are found and in 20 families the perforation is mainly simple but a few scalariform perforation plates (usually short) can be found.

From all the above facts it appears that in the dicotyledons the vessels arose first in woody plants. Apparently they developed independently a number of times as vessel-less species are found in different families. Because of the advanced character of the vessels in herbaceous plants it cannot be suggested that the woody plants have been derived from the herbaceous plants.

As a result of the data that have accumulated, it has been concluded that the vessels arose first in the secondary xylem and later in the metaxylem. The specialization has also gradually advanced from the secondary to primary xylem.

It can also be assumed that the herbaceous plants have developed from the woody plants by reduction of cambial activity only after obvious development of the vessel members had taken place in the woody ancestral plants.

In some specialized dicotyledons, such as certain of the Cactaceae, the secondary xylem lacks vessels which are replaced by so-called vascular tracheids. However, in such plants the lack of vessel elements is a result of secondary reduction (Bailey, 1957).

Monocotyledons

1. From a phylogenetic point of view, vessels in the monocotyledons first appeared in the roots and later in the stems and leaves. The specialization of the vessels followed the same pattern (Cheadle, 1943a, b).

2. Phylogenetically, the vessels first appeared and became specialized in the late-formed metaxylem and progressed gradually into the early-formed metaxylem and finally into the protoxylem (Cheadle, 1944).

3. Monocotyledons exist today that have, in the last-formed metaxylem of their roots, only the most primitive vessels the perforation plates of which are scalariform and which contain more than 100 parallel perforations.

4. A few monocotyledonous families with only aquatic species are known to include plants that lack vessels completely in all their organs. This feature, however, may be a secondary one.

The tracheary elements have developed during the evolution of the land plants. As has been pointed out by Bailey (1953), two main functional trends have become evident during the course of the morphological evolution of these elements, i.e. the development of those structures that enhance rapid conduction, on the one hand, and of those that strengthen the elements, on the other hand. These two trends are antagonistic to a great extent because certain structures that increase the efficiency of conduction tend to weaken the cells and vice versa. However, during the course of evolution, structures have been developed that have, to various extents, resolved these two trends.

Pitted tracheary elements, in addition to those with annular and helical wall thickenings, are found in most of the Tracheophyta, with the exception of certain lower Devonian plants and some hydrophytes. Elements with such wall thickenings give support to the mature stem. The absence of living protoplasts in the tracheary elements, the development of elongated tracheids and the occurrence of vessel members are all features that increase the efficiency of water conduction. The bordered pit-pairs which are characteristic of the tracheary elements, are, as has been shown by Bailey, well adapted to their function and they combine the two above-mentioned trends. On the one hand, the area of the pit membrane is comparatively large and so the passage of water is fairly easy and, on the other hand, the extent of the development of the secondary wall is maximal because the secondary wall overarches the pit membrane in such a manner that the pit membrane remains comparatively large whereas the pit aperture is very small. This feature greatly strengthens the tracheary elements.

In tracheids more rapid conduction is obtained by the elongation of the cells, the increase in diameter of the lumen and in the number of pits and the reduction of wall thickness. Strengthening of the tissue is brought about by the shortening of the cells, narrowing of the lumen, increase in wall thickness and the reduction in the number of pits. In the secondary xylem of conifers, for instance, the early wood is more adapted for efficient water conduction and the tracheids of the late wood, for support.

Conduction is further facilitated by the complete disappearance of the pit membranes in certain areas so resulting in the formation of vessel members. In the secondary xylem of certain primitive dicotyledons primi-

tive vessel members, resembling scalariform pitted tracheids, and thick-walled, narrow tracheids with a few round bordered pits have been observed to occur side by side. This phenomenon proves that the evolution of tracheids, in relation to function, was dichotomous, i.e. the scalariform tracheids evolved into vessel members which were better adapted to conduction, whereas the tracheids with round bordered pits are modified to give better support and, through various intermediate forms, give rise to the libriform fibres. Fibre-tracheids, which are an intermediate form, and libriform fibres functionally differ greatly from the tracheary elements and in many plants they contain even living protoplasts and store reserve materials.

From the large amount of data that has been accumulated from the study of the various angiosperm groups, it is possible to build a clear picture of the trend of evolution as has taken place in the development of the tracheary elements. The fact that this trend is unidirectional, irreversible and cannot be interpreted in the reverse direction is important and should be emphasized. The structural evolution of the tracheary elements presents one of the most convincing examples of evolutionary development. However, although it is obvious from the great amount of data, that this structural evolution has been accompanied by functional specialization, as yet almost nothing is known about whether or not a correlation exists between the types of tracheary elements and ecological conditions. This is a problem that still needs to be investigated.

The sequence of the different types of tracheary elements and the numerous transitional forms are important features in the study of the origin of the Angiospermae and the phylogeny of the various taxonomic groups among them. It is still necessary, however, because of parallel and convergent evolution, to accumulate more data concerning the tracheary elements of the various species and to use such data together with morphological and structural data concerning other elements and tissues, before any definite conclusions can be drawn (Fahn, 1954).

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CHAPTER 8

PHLOEM

THE phloem together with the xylem constitute the conducting system of vascular plants. The xylem functions principally in the conduction of water, and the phloem of products of photosynthesis. Similarly to the xylem the phloem also is a compound tissue. The important cells of the phloem are the *sieve elements* which serve for the conduction of the photosynthetic products. Additional to these elements phloem contains typical parenchyma cells in which reserve substances are stored, as well as specialized parenchyma cells, i.e. the *companion cells* and *albuminous cells*, which are connected with the functioning of the sieve elements. Fibres, sclereids and sometimes laticifers may also be found in phloem tissue.

The primary phloem, similarly to the primary xylem, develops from the procambium. The primary phloem is divided into the *protophloem*, which develops from the procambium during an early ontogenetic stage, and the *metaphloem* which also develops from the procambium, but at a later stage of development.

The sieve elements were first discovered by Hartig in 1837 and the term phloem was coined, from the Greek word for bark, by Nägeli in 1858.

The phloem in the stem, is usually external to the xylem but in some ferns and in different species of numerous dicotyledonous families, e.g. Asclepiadaceae, Cucurbitaceae, Myrtaceae, Apocynaceae, Convolvulaceae, Compositae and Solanaceae, phloem is also present on the inside of the xylem. Phloem on the inside of the xylem is called *internal* or *intraxylary phloem* (Fig. 70, no. 3) and it develops a little later than the external phloem. In certain families, such as the Chenopodiaceae, Amaranthaceae, Nyctaginaceae, Salvadoraceae and others, phloem is also present within the secondary xylem. This type of phloem is called *interxylary phloem* or *included phloem* (Fig. 158, nos. 1–3).

Sieve elements

The most characteristic features of sieve elements are the *sieve areas* in the walls and the disappearance of the nucleus from the protoplast.

The sieve areas are interpreted as being modified primary pit fields and they appear as depressions in the wall in which groups of pores are located. *Connecting strands*, which are structures resembling plasmodesmata but which are thicker, pass through these pores and so connect the protoplasts of the neighbouring sieve elements (Fig. 50, no. 1; Fig. 51, no. 1). Sieve areas can be distinguished from primary pit fields by the following two features: (a) in the sieve areas the connecting strands are much thicker than the plasmodesmata that occur in the primary pit fields; (b) in the sieve area each pore contains a small cylinder of *callose* which surrounds the connecting strand (Fig. 48, nos. 2–4; Fig. 51, no. 1). The diameter of the pores varies in the different species from a fraction of a micron to 14 μ. In *Spiraea vanhouttei* the diameter of the pores is less than 1 μ while in *Pyrus malus* and *Pyrus communis* the maximum diameter is only a little larger than 1 μ, in *Curcubita* spp. it is 10·3 μ and in *Ailanthus altissima*, 14·3 μ (Esau and Cheadle, 1959). The presence of callose can easily be demonstrated by staining with aniline blue or resorcin blue (Esau, 1948). In ultraviolet light even minute amounts of callose stained with aniline blue give a lemon-yellow fluorescence. Callose also occurs on the walls of fungal cells, in the germination tube of pollen grains, in cystoliths, and recently, has even been shown to be present in the primary pit fields of epidermal cells (Currier and Strugger, 1956).

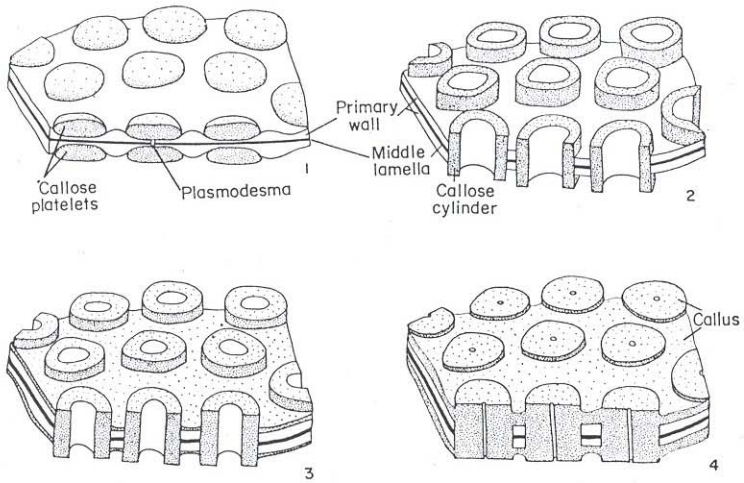

FIG. 48. Diagrams showing development and maturation of a portion of a sieve plate. 1, Early stage showing appearance of callose platelets. 2, The pores are lined by relatively thin callose cylinders. 3, The callose cylinders have thickened and callose has been deposited on the surface of the plate between the cylinders. 4, Sieve plate with definitive callus.

Callose is a polysaccharide built of D-glucose residues (Frey-Wyssling *et al.*, 1957). More accurate analysis has shown that in *Vitis* the callose

consists of β-D-glucopyranose residues with 1:3 linkages (Aspinall and Kessler, 1957). Callose is also found on those portions of the wall between the callose cylinders surrounding the connecting strands. In old elements large amounts of callose accumulate to form continuous thick layers which were termed *callus* by Hanstein in 1864. This term callus should not be confused with that referring to wound tissue.

In sieve areas that are not highly specialized the connecting strands are extremely thin and are nearly indistinguishable from plasmodesmata. In highly specialized sieve areas the connecting strands are very thick and they stain intensely. When the sieve element is young, the sieve area is thinner than the other portions of the cell wall and it appears as a depression on the inner surface of the wall. As the element matures additional callose is laid down not only on the cylinders, which line the pores, but also on the surface of the sieve area between the pores, so that finally, in old elements, the sieve areas do not appear as depressions but as raised portions above the surface. When the element ceases to function the connecting strands become very thin and may even disappear. When sieve areas develop close to one another the callose masses from each sieve area may fuse to form a single mass. Large masses of callose which develop with the cessation of function of the elements are called *definitive callus* (Fig. 49, no. 1). Usually, with the complete disintegration of the protoplast of the element the callus peels away from the sieve areas. In most dicotyledons the sieve elements function during a single growing season, but in certain plants, such as *Suaeda*, *Tilia* and *Vitis*, the sieve elements function for two or more years. In *Tilia* no distinct changes can be seen in the sieve elements with the start of the resting season, while in *Vitis* large amounts of callus accumulate in the autumn, disintegrate in the spring before the commencement of cambial activity, and so the sieve elements start to function for a second year (Esau, 1948; Bernstein and Fahn, 1960).

The density and arrangement of the sieve areas on the sieve elements exhibit the same degree of variation as does the pitting on the walls of the tracheary elements. On the basis of the thickness of the connecting strands and the degree of development of the callose cylinders, sieve areas with different stages of specialization can be distinguished. In certain plants, such as the Coniferales, all the sieve areas of an element are equal, while in other plants, for instance, most of the angiosperms, some of the sieve areas are more specialized, i.e. they have more well-developed connecting strands and callose cylinders than those found in other areas. These more specialized sieve areas are usually situated on the end walls of the elements which are horizontal or oblique to the longitudinal axis of the element. Those parts of the cell wall that bear such specialized sieve areas are called *sieve plates* (Fig. 49, no. 3).

Two theories exist as to the manner in which the pores of the si ve plate develop. According to one theory the sieve plates develop fromeprimary

pit fields and then the connecting strands are derived from a single or a group of plasmodesmata. According to the second theory the pore sites of the future sieve plates contain no plasmodesmata and the formation of the pores involves the dissolution of the wall at the pore site.

According to Esau *et al.* (1962), the sites of the future pores are first delimited by the appearance of small deposits of callose in the form of

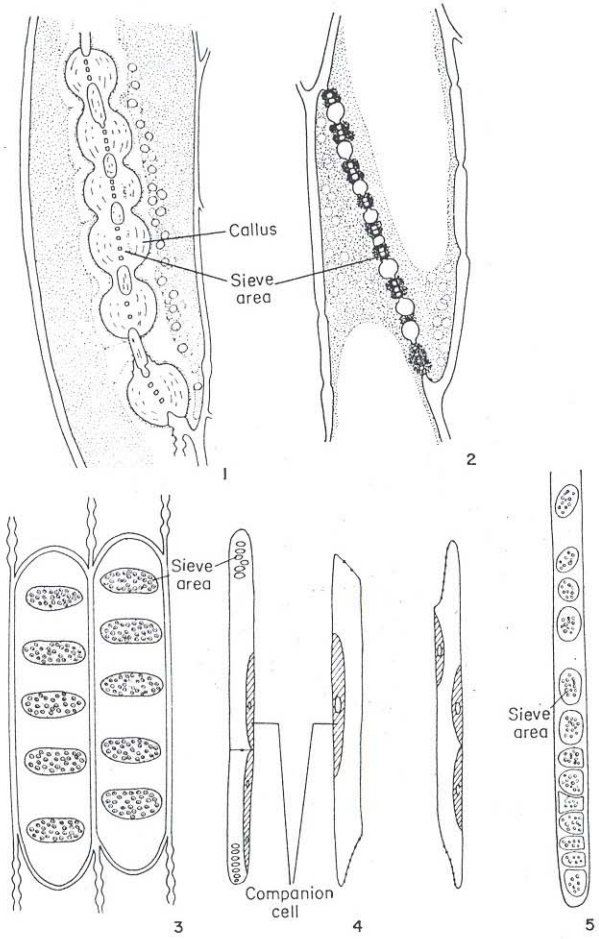

FIG. 49. 1–4, Sieve-tube members of *Vitis*. 1 and 2, Longitudinal sections of compound sieve plates between two elements. 1, Elements in dormant state in which the plate is covered by a thick layer of callus. 2, Elements reactivated after the removal of the callus. The slime which fills the sieve areas is indicated by heavy stippling. 3, Surface view of two compound sieve plates. 4, Sieve-tube elements with companion cells. 5, Portion of a sieve cell of *Pinus*. (Nos. 1–4, adapted from Esau, 1948.)

platelets. Apparently, the formation of the callose platelets takes place after the endoplasmic reticulum approaches the developing sieve plate. The callose platelets are paired and the two members of such a pair occur on the opposite sides of a sieve plate where they are separated from each other by thin portions of the wall consisting of the middle lamella and parts of the primary walls of the two adjacent cells (Fig. 48, no. 1). The

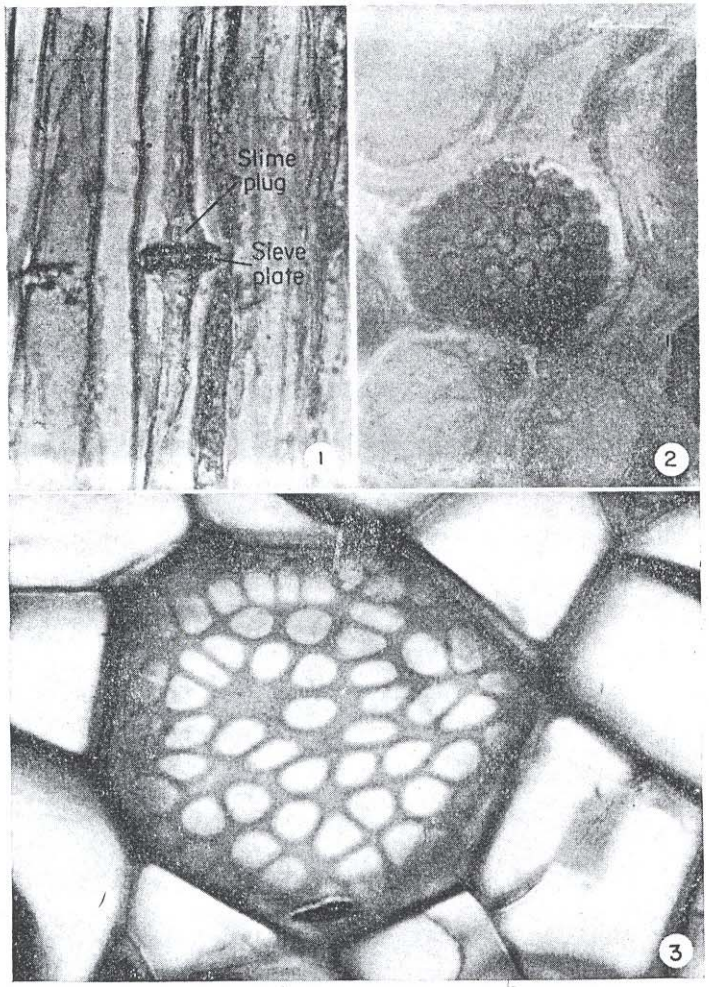

FIG. 50. 1, Micrograph of a longitudinal section in phloem of *Cucurbita*, stained with aniline blue, in which slime plugs can be distinguished. ×440. 2, Surface view of a sieve plate showing the pores lined by cylinders of callose; stained with aniline blue. ×640. 3, Surface view of a sieve plate showing the large pores; stained with safranin-fast green. ×880.

platelets increase in diameter, whereas the cellulosic bars between the pore sites decrease in width. These cellulosic bars together form the basic network of the sieve plate. The platelets and the bars increase in thickness. It appears that there is a single plasmodesma in each pore site. The perforation occurs in the centre of each platelet in that position where the thin wall dissolves. The callose platelets of each pair fuse around the perforation and thus each pore is lined with callose from its inception. Later, callose appears also on the surface of the sieve plate. The perforation of the sieve plate takes place after the disintegration of the nucleus.

Those sieve elements that have unspecialized sieve areas that are similar throughout the element are called *sieve cells* (Fig. 49, no. 5). Sieve cells,

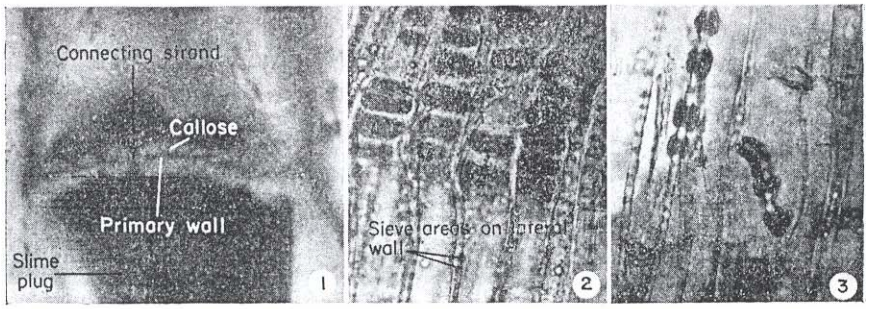

FIG. 51. 1, Cross-section of a sieve plate of *Cucurbita*. ×1200. 2 and 3, Compound sieve plates in secondary phloem of *Vitis*. 2, Surface view as seen in radial longitudinal sections of phloem. ×265. 3, Cross-section of plate as seen in tangential longitudinal section of phloem. ×265.

therefore, do not contain sieve plates. These cells are usually elongated with tapering ends or their end walls are very oblique. In the positions where sieve cells overlap one another the sieve areas are more numerous.

Elements in which sieve plates can be distinguished are called *sieve-tube members* (Fig. 49, no. 4). Sieve plates are usually found on the end walls which may be very oblique or horizontal or in intermediate planes. In certain elements, e.g. those of *Vitis* and *Pyrus malus*, the sieve plate contains several sieve areas; while in other elements, e.g. those of *Cucurbita*, only one sieve area may be present. The former type of sieve plate is termed a *compound sieve plate* (Fig. 49, nos. 1–4; Fig. 51, nos. 2, 3) and the latter, a *simple sieve plate* (Fig. 50, nos. 1–3). The sieve-tube members are connected one to the other by the walls that contain the sieve plates and so form *sieve tubes*. Sieve plates are found only very occasionally on the longitudinal walls of the sieve-tube members. On these walls unspecialized sieve areas develop.

THE CELL WALL

The walls of sieve elements are usually only primary and consist mainly of cellulose. Only in a single family of the Coniferales, the Pinaceae, has a secondary, non-lignified cell wall been found in the sieve cells (Abbe and Crafts, 1939). The thickness of the wall of the sieve elements varies in different species; in some species the cell wall is 1 μ thick while in other species the wall nearly fills the cell lumen. Esau and Cheadle (1958) also found differences in the structure of the wall. In certain species they found that the wall is homogeneous, while in others the wall is composed of two layers—a thin layer close to the middle lamella and a thicker layer next to the cytoplasm. The inner layer as seen in cross-sections of fresh material has a sheen similar to mother-of-pearl, and therefore has been termed the *nacreous* layer. The thickness of the wall of the sieve elements usually decreases with the aging of the element. Thick nacreous walls can be seen, for example, in *Magnolia*, *Laurus*, *Rhamnus* and *Persea* but they are not present in *Casuarina*, *Crataegus*, *Fraxinus*, *Morus*, *Populus*, *Salix* and *Passiflora*, among others.

THE PROTOPLAST

The most characteristic feature of the protoplast of the sieve element is the absence of a nucleus in the mature, active cell. The structure of immature sieve elements resembles that of the procambial and cambial cells from which they develop. In this stage the protoplast contains vacuoles and a large nucleus. With the specialization of the element the nucleus disintegrates and disappears. In certain plants the nucleolus or nucleoli are extruded from the nucleus prior to its disintegration and they remain within the sieve element.

A more or less viscous substance, which stains readily with cytoplasmic stains, is present in the sieve-tube members of dicotyledons. This substance has been termed *slime*. It is thought that slime is of a proteinaceous nature. It is located in the vacoule and in the preparation of sections it accumulates at the ends of the cells near the sieve plates. These slime accumulations are termed *slime plugs* (Fig. 50, no. 1; Fig. 51, no.1). The slime is produced in the cytoplasm in the form of small, variously shaped slime bodies that, with the specialization of the sieve element, become more liquid and pass into the vacuole where they become amorphous. This process takes place at the same time as the disintegration of the nucleus. In monocotyledons, gymnosperms and pteridophytes slime bodies have not been observed, and in these plants the vacuole of the sieve elements is aqueous with only small quantities of slime.

In the sieve elements of many species small plastids that take part in the synthesis of carbohydrate granules are present. These granules are similar to starch but stain red with iodine, and apparently contain a high

percentage of dextrins. In sections these granules accumulate, together with the slime, near the sieve areas.

It is difficult to get an accurate picture of the structure of the protoplast in a mature sieve element from the study of microscope sections because of the changes in position of the protoplasmic constituents that take place during sectioning. The cell contents are pushed in the direction of the cuts, and a portion may even be extruded onto the surface of the section by a pressure that exists in the mature sieve element. Under the microscope it is seen that the slime content of the vacuoles accumulates near those sieve areas close to the cuts and it appears as if this substance passes through the sieve areas. In order to avoid these artifacts investigators have used special fixation and other methods prior to sectioning.

The accepted view today is that there is a thin cytoplasmic layer lining the inner surface of the cell wall and the centre of the cell is occupied by a large central vacoule which contains the cell sap and different quantities of slime. The protoplasts devoid of nuclei are firmly attached to the sieve areas by the connecting strands (Esau, 1950). During the maturation of the sieve element the border between the vacuole and the cytoplasm disappears. From electron microscope studies it has been seen, during the nuclear disintegration, that the other organelles, the endoplasmic reticulum and the tonoplast become more or less disorganized. The plasmalemma and the remnants of the other cytoplasmic structures constitute the thin parietal cytoplasmic layer of the mature element (Esau and Cheadle, 1962). These and other features indicate reduced metabolic activity in the mature sieve elements.

Different opinions exist as to the nature of the connecting strands. According to one opinion these strands are entirely cytoplasmic, while according to another they contain vacuolar substances which serve as the connection between the vacuoles of the neighbouring elements. The latter view, i.e. that of vacuolar continuity, is the more accepted one today.

Different and contrary theories also exist as to the method of conduction of the photosynthetic products in the sieve elements (Esau *et al.*, 1957). According to one theory these substances are conducted through the sieve elements by a *mass flow* which is the result of the differences in hydrostatic pressure between the supplying and receiving organs. This theory was first formulated by Münch in 1930 and can be demonstrated by the following model. When an osmotic cell containing solutes is placed in water, water enters into it. The level of the solution in the osmometer will rise until equilibrium is reached between the hydrostatic and osmotic pressures. If two osmometers with solutions of different osmotic pressures are used, it is seen that the solution rises less in that osmometer with the lower osmotic pressure. If the two osmometers are connected there will be a flow from that osmometer with the higher osmotic pressure to that with the lower. This flow is a result of the pressure gradient between the two

osmometers. In the above case, molecules of solute flow passively with the solvent. Therefore, according to the theory of mass flow, the molecules of sugar and other dissolved substances are conducted through the phloem as a result of the flow of the aqueous solution. Thus the force, which enables the flow, is a result of the differences in the osmotic pressure between the supplying organs (the leaves) and the receiving organs (the roots, tubers, etc.). Supporters of this theory regard the phloem as the tube that connects the above-mentioned osmometers, as the cytoplasm in these elements, contrary to that of other cells, is permeable to the products of photosynthesis (Huber, 1941). According to these investigators the cytoplasm of the sieve elements lacks a tonoplast, is incapable of accumulating "neutral red" and does not plasmolyse when the cells are placed in a hypertonic solution.

Another theory is that of the active transport of the solutes. The supporters of this theory are of the opinion that the cytoplasm of the sieve elements takes an active part in the transfer of the substances. They suggest that the protoplasts of the sieve elements have the property of selective permeability, and they explain the difficulty of demonstrating plasmolysis of these cells by the particular sensitivity of the nucleus-free protoplast which therefore necessarily demands extremely careful treatment (Rouschal, 1941).

It is accepted by all workers that the passage of photosynthates in the sieve elements is much faster than that in ordinary parenchyma cells.

Phylogeny of sieve elements

In the most primitive form the sieve elements are parenchyma cells that have undergone modifications in connection with their function. This was followed by the loss of the nucleus. This protoplasmic specialization apparently resulted in the development of the interdependence of the sieve elements and parenchyma cells that retain their nucleus, i.e. the albuminous cells in the gymnosperms and the companion cells in the angiosperms. In the angiosperms the sieve elements and companion cells develop from the same mother cell. The specialization of the sieve elements also involved the development of thick connecting strands. In pteridophytes and gymosperms these strands are thin and resemble plasmodesmata, while in the angiosperms they are thick and conspicuous. The evolutionary trends in the shape of the sieve elements and the arrangement of sieve areas have been more thoroughly studied in the monocotyledons (Cheadle and Whitford, 1941; Cheadle, 1948; Cheadle and Uhl, 1948). The specialization, in this group of plants, has taken the following courses: (1) gradual localization of highly specialized sieve areas to the end walls of the elements; (2) gradual changes in the position of the end wall from very

oblique to horizontal; (3) gradual change from compound sieve plates to simple ones; (4) gradual reduction of the sieve areas on the side walls of the elements. In monocotyledons the above investigators also found that the sieve tubes first developed in the aerial portions of the plants from where the development and specialization spread to the roots. This direction of development is opposite to that of the development of the vessels in the xylem. This phenomenon is understandable from a functional point of view. Features of the dicotyledonous sieve-tube members suggest that the phylogenetic development in this group of plants is similar to that of the monocotyledons, but as yet no conclusive research has been done. According to Zahur (1959), the sieve-tube elements in the angiosperms, like the vessel elements, have undergone a decrease in length during the course of evolution.

Companion and albuminous cells

Sieve-tube members of the angiosperms are accompained by highly specialized parenchyma cells which are termed *companion cells* (Fig. 49, no. 4). These cells retain the nuclei throughout their life. The above two types of elements, i.e. the sieve-tube members and the companion cells, are related ontogenetically as they develop from the same meristematic cell. Such a meristematic cell divides longitudinally once or several times and one of the resulting cells, usually the largest, specializes to form the sieve-tube member and the others develop directly or indirectly, by further transverse or longitudinal divisions, into the companion cells. One or more companion cells may accompany a sieve-tube member. Companion cells vary in size—they may be as long as the sieve-tube member to which they are related or they may be shorter. Companion cells may develop on various sides of the sieve tube or they may form longitudinal rows on one side only. Companion cells are strongly attached to the sieve-tube members from which they usually cannot be separated even by maceration. The walls between sieve-tube members and the companion cells are thin or possess many thin areas which, apparently, are sieve areas on the side of the sieve-tube member and primary pit fields on the side of the companion cell. The length of life of the companion cells is usually the same as that of the sieve-tube member to which they are attached. This feature proves not only the ontogenetic connection but also the functional connection that exists between these cells. The companion cells and also the phloem parenchyma play an important part in the maintenance of a pressure gradient in the sieve tubes (Esau, 1961).

The protoplast of mature companion cells stains more intensely than that of ordinary parenchyma cells. It is thought that this staining property is due to the presence of a substance similar to that of the slime of the sieve-

tube members. Esau (1947, 1948) found slime bodies in the companion cells of *Vitis* and observed that, with the dispersal of this slime, the protoplast stained more intensely.

Starch has not been found in companion cells.

In pteridophytes and gymnosperms companion cells, as described above, do not occur, but cells which stain intensely with cytoplasmic stains are present. These cells are apparently connected physiologically and morphologically to the sieve cells and have been termed *albuminous cells*. Ontogenetically these cells develop from the phloem parenchyma or from cells of the phloem rays. Albuminous cells do not contain starch during the period that the phloem is active, but they may store it during the rest period.

Protophloem and metaphloem

The primary phloem, as described previously, consists of protophloem nad metaphloem. The protophloem, together with protoxylem, constitutes the vascular tissue of the young elongating parts of the plant.

The description of phloem elements given above refers only to metaphloem and secondary phloem. Sieve areas cannot be distinguished in the protophloem elements of gymnosperms. In angiosperms there are sieve-tube members in the protophloem but, in may plants, there are no companion cells. These sieve-tube members are long and narrow, and sieve areas can be distinguished only with difficulty. The walls are somewhat thick and the cell contents stain only slightly. The sieve tubes of the protophloem are apparently active for a short period only. As the sieve-tube members have no nucleus they cannot divide and grow with the elongating organ and so they become obliterated by the surrounding cells. The remnants of these obliterated cells may completely disappear in time. In many dicotyledonous stems the parenchyma of the protophloem remains after the obliteration of the sieve-tube members, and then these cells become fibres. In leaves they form elongated collenchyma cells.

In contrast to those sieve elements of the protophloem which only function for a short period and which are early obliterated, the sieve elements of the metaphloem of the Pteridophyta and long-living monocotyledons, such as the Palmae, apparently function for many years.

When fibres occur in the primary phloem of dicotyledonous plants they are always restricted to the protophloem even in those cases where fibres develop later in the secondary phloem of the same plant.

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