The walls of both kinds of parenchyma cells have numerous primary pit-fields interconnecting axial parenchyma cells and ray cells with one another and among themselves. Pit-fields also occur between parenchyma cells and companion cells and between parenchyma cells and sieve elements. Usually the pit-field on the sieve element side is called a sieve area since it develops callose.

Fibers

The fundamental structure of phloem fibers, their origin, and their development were considered in chapter 10 (see also Esau, 1950). Fibers occur in both primary and secondary phloem. Those of the primary commonly develop in organs that are still elongating. By a combination of symplastic and apical intrusive growth, the primary fibers may become very long. The secondary phloem fibers arise from fusiform cambial cells as components of the axial system. These fibers may elongate by apical intrusive growth, but, as a rule, they remain conspicuously shorter than the primary fibers of the same plant. The primary and the secondary phloem fibers develop secondary walls after they complete their elongation, although the beginning of secondary-wall deposition may occur while the cell is still elongating at its apices (chapter 10). In some plants the fibers are typically lignified; in others they are not. The pits in their walls are usually simple, but may be slightly bordered. Septate and gelatinous fibers also occur in the phloem. In some plant species the secondary phloem fibers mature in the conducting phloem and appear to be highly specialized as mechanical elements (*Tilia*). In other species they have primary walls and active protoplasts in the functioning phloem and differentiate as fibers only after the sieve elements cease to function (*Prunus*, pl. 44*B*; *Parthenium*). Some workers consider such fibers to be sclerotic phloem parenchyma cells, or sclereids, and not true fibers (Holdheide, 1951). When a sclerenchyma cell has characteristics intermediate between fibers and sclereids it may be called fiber-sclereid (Evert, 1963*a*). Phloem fibers, like xylem fibers, may remain alive and store starch (septate fibers in *Vitis*, pl. 44*A*).

PRIMARY PHLOEM

In conformity with the classification of the primary xylem into protoxylem and metaxylem, the primary phloem may be divided into *protophloem* and *metaphloem*. These terms have evolved in relation to the parallel terminology for the primary xylem (chapter 11).

Protophloem

The protophloem constitutes the conducting tissue of the actively growing parts of the plant and contains sieve elements possessing the usual specialized characteristics of such elements, that is, highly vacuolate, enucleate protoplasts and walls bearing sieve areas. There is some doubt regarding the morphologic nature of the first phloem elements in the gymnosperms and since no sieve areas have been recognized in them they are referred to as *precursory phloem* cells (pl. 54*A*; Esau, 1950; Smith, 1958). In the angiosperms, sieve elements have been observed in the protophloem of roots, stems, and leaves in woody and herbaceous species (Esau, 1939, 1950). These elements appear to be sieve-tube members, but they may lack companion cells. They are elongated but have narrow transverse diameters, and their sieve areas are revealed only in good preparations and at high magnifications. The recognition of these elements is frequently facilitated by their somewhat thickened walls, which readily absorb cellulose stains (pl. 45*A*), and by the scarcity of stainable contents in their lumina. The light staining of contents often makes the sieve elements particularly conspicuous among the adjacent protophloem cells still possessing dense protoplasts.

The sieve tubes of the protophloem apparently function for a brief period only. In rapidly elongating organs they are destroyed (fig. 10.2*B*, pl. 45*B*), soon after maturation, by the effects of elongation of the surrounding cells. Being enucleate cells they are unable to keep pace with this growth by active elongation and are passively stretched. Often the surrounding cells crush both the partly stretched elements and their companion cells, if such are present. The remnants of the crushed cells may later disappear completely. This phenomenon of effacement of the sieve elements is commonly called obliteration.

In many dicotyledons the cells remaining in the protophloem after the sieve tubes are obliterated differentiate into fibers (Blyth, 1958; Léger, 1897). Certain vine types of stems, which possess a sclerenchyma cylinder outside the vascular strands (*Aristolochia, Cucurbita;* figs. 10.1*H*, 12.1), form no fibers in the protophloem. In the leaf blades and the petioles of dicotyledons the protophloem cells remaining after the destruction of the sieve tubes often differentiate into long cells with collenchymatically thickened unlignified walls (chapter 9). The strands of these cells appear, in transverse sections, like bundle caps delimiting the vascular bundles on their abaxial sides. This type of transformation of the protophloem in leaves is widely distributed and occurs also in those species that have protophloem fibers in the stems (Esau, 1950). As was pointed out in chapter 10, the profound change that the protophloem undergoes during the early stages of development of an organ

obscures the original nature of the tissue and may lead to the erroneous assumption that this tissue is distinct from the rest of the phloem and constitutes part of the so-called pericycle (Blyth, 1958).

Metaphloem

Since the metaphloem matures after the growth in length of the surrounding tissues is completed, it is retained as a conducting tissue longer than the protophloem. Some herbaceous dicotyledons, most monocotyledons, and many lower vascular plants produce no secondary tissues and depend entirely on the metaphloem for food conduction after their primary bodies are fully developed. In woody and herbaceous species having cambial secondary growth the metaphloem sieve elements become inactive after the secondary conducting elements differentiate. In such plants the metaphloem sieve elements may be partly crushed or completely obliterated.

The absence of secondary growth in persisting plants, such as ferns, bamboo, and palms, raises the question whether these plants have sieve elements which, despite their enucleate protoplasts, remain functional for many years. The scanty references to this subject (Esau, 1939) suggest that such protracted longevity might occur.

The sieve elements of the metaphloem (pl. 45*C*) are commonly longer and wider than those of the protophloem, and their sieve areas are more distinct. In the angiosperms investigated thus far, these elements are sieve-tube members. Companion cells and phloem parenchyma are typically present in the metaphloem of the dicotyledons. In the monocotyledons, the sieve tubes and companion cells often form strands containing no phloem parenchyma cells among them, although such cells may be present on the periphery of the strands (Cheadle and Uhl, 1948). In such phloem the sieve elements and companion cells form a regular pattern, a feature that is considered to be phylogenetically advanced (Carlquist, 1961). A monocotyledonous type of metaphloem, without phloem parenchyma cells among the sieve tubes, may be found in herbaceous dicotyledons (Ranunculaceae, chapter 15).

According to the literature, the metaphloem of dicotyledons usually lacks fibers (Esau, 1950). If primary phloem fibers occur in dicotyledons, they arise in the protophloem, but not in the metaphloem, even if such elements are later formed in the secondary phloem. In herbaceous species the old metaphloem may become strongly sclerified. Whether the cells undergoing such sclerification should be classified as fibers or as sclerotic phloem parenchyma has not been determined. In monocotyledons sclerenchyma encloses the vascular bundles as bundle sheaths and may also be present in the metaphloem (Cheadle and Uhl, 1948).

The delimitation between protophloem and metaphloem is sometimes rather clear, as, for example, in the aerial parts of monocotyledons having only sieve tubes in the protophloem and distinct companion cells associated with the sieve tubes in the metaphloem (pl. 57*B*). In dicotyledons the two tissues usually merge gradually, and their delimitation must be based on a developmental study.

In plants having secondary phloem the distinction between this tissue and the metaphloem may be quite uncertain. The delimitation of the two tissues is particularly difficult if radial seriation of cells occurs in both tissues. An exception has been found in *Prunus*, in which the last cells initiated on the phloem side by the procambium mature as large parenchyma cells and sharply delimit the primary from the secondary phloem (chapter 15; Schneider, 1945). In general, the developmental relations between the two parts of the phloem have not been sufficiently investigated. No data are available on the relative lengths of primary and secondary sieve elements comparable to those assembled for the tracheary elements, which prove that the last metaxylem cells are distinctly longer than the first secondary elements (chapter 11).

SECONDARY PHLOEM

Basic Structure

The arrangement of cells in the secondary phloem parallels that in the secondary xylem. A vertical or axial system of cells, derived from the fusiform initials of the cambium, is interpenetrated by the transverse or ray system derived from the ray initials (figs. 12.7–12.10; pls. 42, 43). The principal components of the axial system are sieve elements (either sieve cells or sieve-tube members, the latter usually with companion cells), phloem parenchyma, and phloem fibers. Those of the transverse system are ray parenchyma cells.

Storied, nonstoried, and intermediate types of arrangement of phloem cells may be found in different species of plants. As in the xylem, the type of arrangement is determined, first, by the morphology of the cambium (that is, whether it is stratified or not) and. second, by the degree of elongation of the various elements of the axial system during tissue differentiation.

Many woody species of dicotyledons show a division of the secondary phloem into seasonal growth increments (Holdheide, 1951), although this division is less clear than in the secondary xylem. The growth layers in the phloem are distinguishable if the cells of the early phloem expand more strongly than those of the late phloem (fig. 12.9*B*, pl. 44*A*; Artschwager, 1950; Holdheide, 1951). In *Pyrus malus* a band of future

fiber-sclereids and crystalliferous cells overwinter in meristematic state near the cambium and when mature can serve as a marker for delimiting the successive growth layers (Evert, 1963*b*). The collapse of the sieve elements in the nonconducting region of the phloem and the concomitant modifications in some other cells—notably the enlargement of the parenchyma cells—contribute toward obscuring the structural differences that might exist in the different parts of a growth layer at its inception (pl. 44*B*). Many gymnosperms and angiosperms form fibers in tangential bands in the secondary phloem (figs. 12.7, 12.8). The number of these bands is not necessarily constant from season to season and cannot be safely used to determine the age of the phloem tissue.

The phloem rays are continuous with the xylem rays since both arise from a common group of ray initials in the cambium. (Compare figs. 12.7 and 12.8 with figs. 11.10 and 11.11.) The phloem ray and the xylem ray together constitute the vascular ray. Near the cambium the phloem and the xylem rays having common origin are usually the same in height and width. However, the older part of the phloem ray, which is displaced outward by the expansion of the secondary body, may increase in width, sometimes very considerably (Holdheide, 1951; pl. 28*A*). Before the phloem rays become dilated their variations in form and size are similar to those of xylem rays in the same species. Phloem rays are uniseriate, biseriate, or multiseriate; they vary in height; and small and large rays may be present in the same species. The rays may be composed of one kind of cell (fig. 12.7), or they may contain both kinds of cell, procumbent and erect (fig. 12.8). Phloem rays do not attain the same lengths as xylem rays, because the vascular cambium produces less phloem than xylem and also because commonly the outer portions of the phloem are sloughed off through the activity of the phellogen.

Conifer Phloem

In conifers the phloem parallels the xylem in the relative simplicity of its structure (fig. 12.7). The axial system contains sieve cells, parenchyma cells, and frequently fibers. The rays are mostly uniseriate and contain parenchyma only or parenchyma and albuminous cells. The cell arrangement is nonstoried. The expansion of cells during differentiation is uniform, the apical elongation slight, and, therefore, the radial seriation of cells, which originates in the cambium, is retained in the mature tissue (pl. 42*C*). In general, conifer phloem seems to show relatively little developmental disturbance in the cell arrangement which it inherits from the cambium.

The sieve cells of conifers are slender, elongated elements comparable