plasts, such as the xylem ray and xylem parenchyma cells, also may have secondary walls. Moreover, cells specialized as mechanical (sclerenchyma) elements may long retain their protoplasts, and cell division is known to occur in the presence of secondary walls (Bailey, 1961). Information is meager on the ability of protoplasts to reduce the thickness of the secondary wall or to modify its chemistry, after the cell completes its development. Delignification and dissolution of secondary walls under normal and pathological conditions have been reported in the literature (Bloch, 1941; Roelofsen, 1959).

The classification into primary and secondary walls was formulated by Kerr and Bailey (1934) and is used widely (Roelofsen, 1959; Wardrop, 1962) but not consistently. Not infrequently the later part of the primary wall, especially if the wall is conspicuously thickened, is called secondary, and the innermost layer of the secondary wall is referred to as tertiary (critique in Bailey, 1957*b*).

Pits

Secondary cell walls are commonly characterized by the presence of depressions or cavities varying in depth, expanse, and detailed structure. Such cavities are termed *pits*. Primary walls also have more or less conspicuous depressions. These differ from the pits in secondary walls in structure and development, and therefore the pits in the secondary walls and the depressions in the primary walls have received different designations (Wardrop, 1962): the secondary walls have *pits*, whereas the primary walls have *primary pit-fields* (Committee on Nomenclature, 1957). Thus, according to this terminology, the meristematic cells and those of their derivatives that form no secondary walls have primary pit-fields (fig. 3.2*D*, pl. 13*B*); cells with secondary walls have pits (fig. 3.2*A*, *B*).

The primary pit-fields of a meristematic cell may be so deeply depressed and so numerous that the wall appears beaded in sectional views. During the differentiation of some cells having only primary walls the primary pit-fields may be but slightly modified; in other, more specialized cells, the primary pit-fields may be considerably changed as the cell matures. In primary pit-fields the primary wall is relatively thin but continuous across the pit-field area. Furthermore, while the cell is alive, the primary pit-fields show concentrations of plasmodesmata (fig. 3.2*D*).

The distinguishing feature of a pit is that the secondary wall layers are completely interrupted at the pit; that is, the primary wall is not covered by secondary layers in the pit region (fig. 3.2*A*). Pits may be formed over primary pit-fields, one or more pit over one field. Such primary pit-fields may remain in evidence after the development of the secondary wall, or they may be obsured when, during the extension growth of the cell, the primary wall is reduced in thickness (Kerr and Bailey, 1934). Pits also arise over primary wall parts that bear no primary pit-fields, and, inversely, some primary pit-fields are completely covered by secondary wall layers. Thus there is no absolute interdependence between the position of the primary pit-fields in the primary wall and the development of pits in the secondary wall.

The distinction between pits and primary pit-fields has a sound morphological basis, but frequently primary and secondary walls cannot be distinguished with ordinary microscopic observation. If an uncertainty exists regarding the exact nature of a wall, neither term, pit or primary pit-field, may be applied without classifying the wall by implication. A substitute term that would include pits and primary pit-fields, however, is not available in the literature. In this book the distinction between pits and primary pit-fields is maintained whenever the nature of the wall is known. If this information is not available but the wall bears clearly circumscribed cavities, these cavities are termed pits. The adjective *pitted* is applied either to secondary walls having pits or to primary walls having primary pit-fields.

It is customary to include in the definition of the pit in a secondary wall not only the cavity but also the part of the primary wall that occurs at the bottom of the cavity (Committee on Nomenclature, 1957). Thus, fundamentally, a pit consists of a *pit cavity* and a *pit membrane.* The pit cavity is open internally to the lumen of the cell and is closed by the pit membrane along the line of junction of two cells (figs. 3.1*C*, *D*; 3.2*A*).

Two principal types of pits are recognized in cells with secondary walls: *simple pits* and *bordered pits.* The most fundamental difference between the two kinds of pits is that in the bordered pit the secondary wall arches over the pit cavity—this part of the wall constitutes the border—and narrows down its opening to the lumen of the cell (fig. 3.3, pl. 11*A*–*C*); in the simple pit no such overarching occurs (figs. 3.1*C*, *D*; 3.2*A*).

A pit in a wall of a given cell usually occurs opposite a complementary pit in the wall of an adjacent cell; that is, two pits are combined into a paired structure, the *pit-pair* (figs. 3.2*A*, 3.3*A*). The pit membrane is common to both pits of a pair and consists of two primary walls and a lamella of intercellular substance (fig. 3.3). Two bordered pits make up a *bordered pit-pair,* two simple pits, a *simple pit-pair.* A bordered pit may be complemented by a simple pit, the two constituting a *half-bordered pit-pair* (pl. 9*A*, *B*). A pit may have no complementary

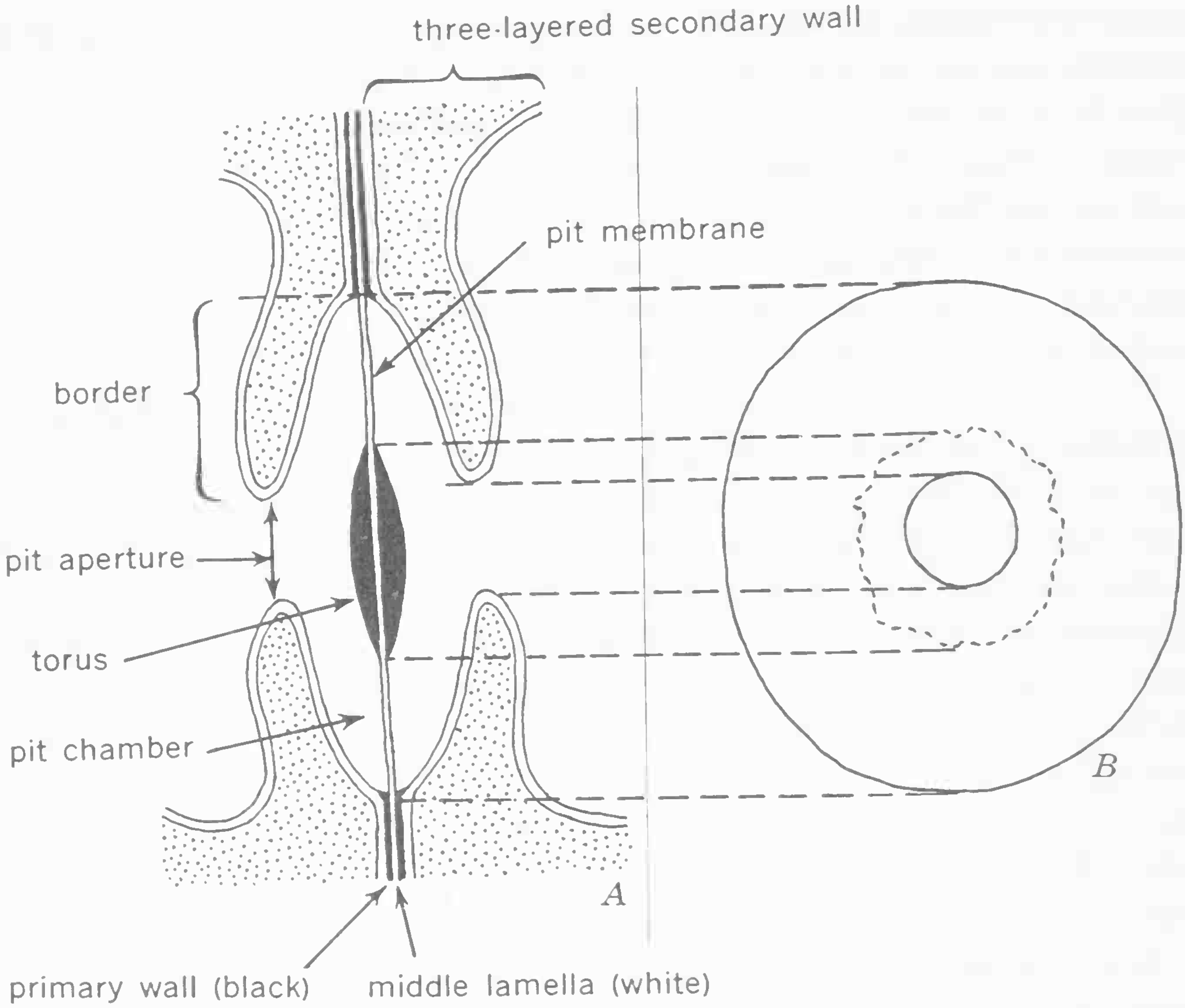


FIG. 3.3. Bordered pit-pair of *Pinus* in sectional (*A*) and face (*B*) views. Details according to the concept of Kerr and Bailey (*Arnold Arboretum Jour.* 15, 1934). The pit membrane consists of two primary walls and the intercellular lamella but is thinner than the same triple structure in the unpitted part of the wall. The torus is formed by thickening of the primary wall. In *B*, outline of torus is uneven.

structure, as, for example, when it occurs opposite an intercellular space. Such a structure is called a *blind pit*. Sometimes two or more small pits are opposed by one pit in the adjacent cell, a combination that has been named *unilaterally compound pitting*.

Simple pits may be found in certain parenchyma cells (fig. 3.2*A*, *B*; pl. 8*B*, *C*), in extraxylary fibers (fig. 3.1*D*), and in sclereids (fig. 3.1*C*). In a simple pit the cavity may be uniform in width, or it may be slightly wider or slightly narrower toward the lumen of the cell. If it narrows down toward the lumen, the simple pit intergrades with the bordered pit in its structure. The simple pits of thin walls are shallow. In thick walls the cavity of a simple pit may have the form of a canal passing from the lumen of the cell toward the pit membrane (fig. 3.1*C*, *D*). Pits may coalesce as the wall increases in thickness and give the impression of a branched canal (fig. 3.1*C*). Such pits are called *ramiform pits* (that is, pits shaped like branches, from the Latin *ramus*, branch).

Bordered pits are more complex and more variable in structure than simple pits. They occur mainly in the water-conducting and mechanical cells of the xylem, such as vessel elements, tracheids, and various fibers, but may be found in some fibers and sclereids outside the xylem also.

The part of the cavity enclosed by the overarching secondary wall, the *pit border*, is called the *pit chamber*, and the opening in the border is the *pit aperture* (fig. 3.3). The pit aperture may be circular, lenticular, or linear (figs. 3.3–3.5). The shape of the aperture may agree with the outline of the pit chamber, or it may not. Vessel elements in the angiosperms often have oval bordered pits with oval apertures (fig. 3.5*B*). Some tracheary cells of ferns have transversely much-elongated bordered pits with linear apertures. In the bordered pits of gymnosperms, circular, oval, or linear apertures may be associated with pit chambers and borders circular in outline (figs. 3.3, 3.4).

If the secondary wall and the border are relatively thick, the border divides the cavity into the pit chamber, the space between the pit membrane and the overarching border, and the *pit canal*, the passage from the cell lumen into the pit chamber (fig. 3.4). Such a canal has an *outer aperture* opening into the pit chamber and an *inner aperture* facing the cell lumen. The two apertures are commonly unlike in shape and size: the inner is rather large, lenticular or linear, the outer small and circular. The thicker the cell wall, the smaller and thicker is the border, the smaller the pit chamber, and the longer and narrower the inner pit aperture. With the increase in wall thickness, the inner aperture may become so long that it may reach laterally the limits of

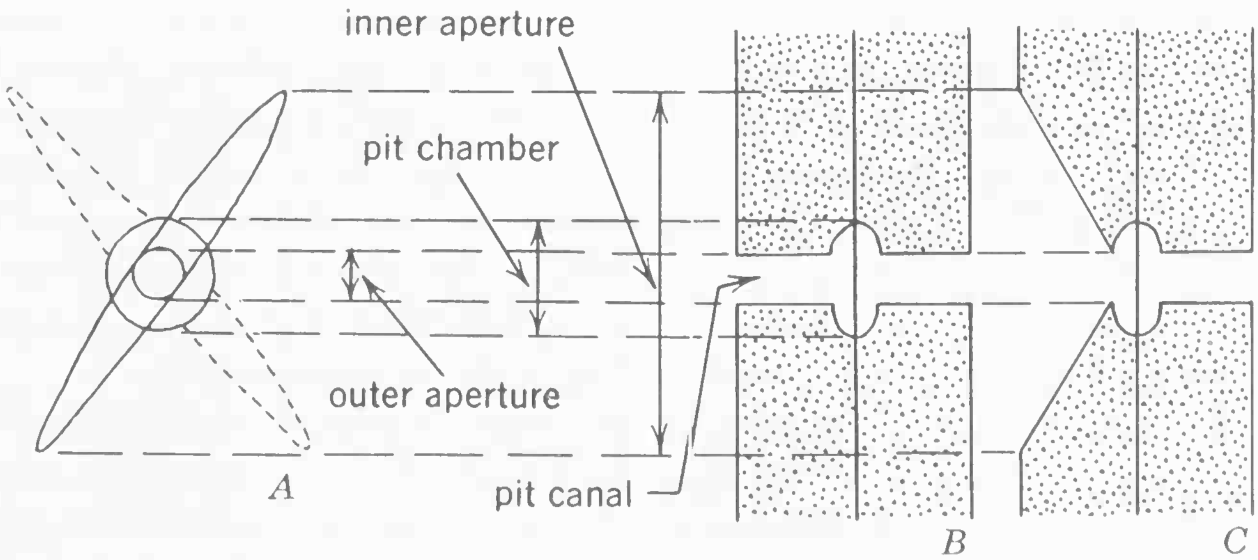


FIG. 3.4. Bordered pit-pair with extended pit apertures, flattened canals, reduced borders, and small pit cavities. *A*, face view showing: extension of pit apertures beyond the limits of pit chamber (or border); crossed arrangement of apertures of the two pits of the pair; and contrast in shape and size of inner and outer apertures. *B*, sectional view exposing pit canal along its short diameter. *C*, sectional view exposing pit canal along its long diameter.

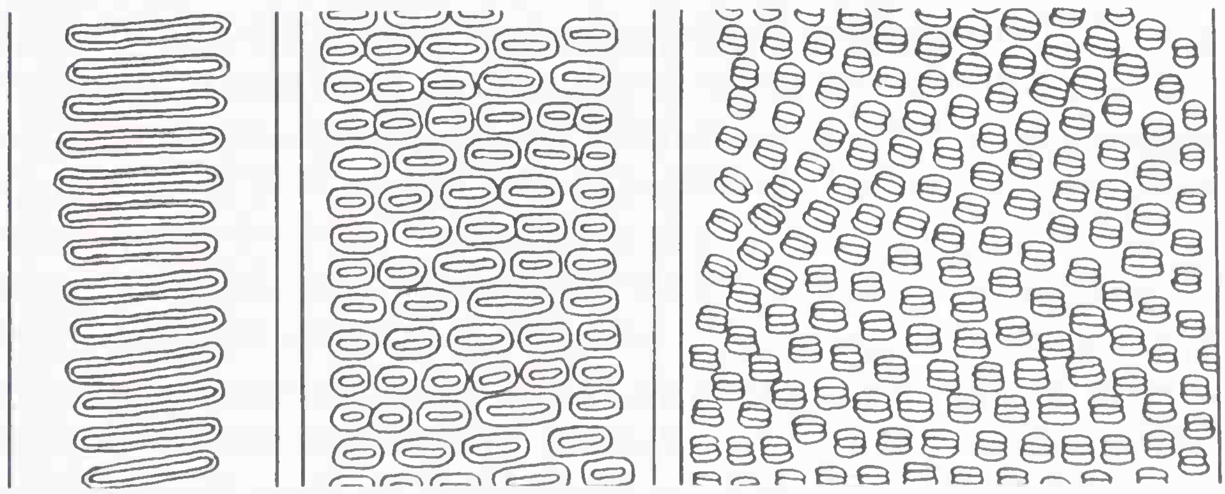
the pit chamber and even surpass these (fig. 3.4). When the inner aperture does not extend beyond the border it is called *included*; when the long diameter of the aperture is longer than the diameter of the border the aperture is called *extended*. If the inner aperture is relatively large and linear or lenticular in outline and the outer is small and circular, the pit canal has the shape of a flattened funnel. The circular pit apertures in a bordered pit-pair appear exactly opposite each other. In a bordered pit-pair with elongated inner pit apertures the apertures may cross each other symmetrically (fig. 3.4*A*).

The bordered pit-pairs of conifer tracheids are particularly elaborate in their structural details (fig. 3.3; pl. 11*A–C*, 12*A*). In the large, relatively thin-walled tracheids of the early wood, these pit-pairs, as seen in face views, have large, circular or oval borders with conspicuous lenticular or circular apertures. The pit chambers are also correspondingly large, with the pit canals practically absent. The pit membrane has a thickening of primary nature, the *torus*, which is somewhat larger in diameter than the pit apertures. The thin part of the membrane surrounding the torus is called *margo* (meaning the edge, or margin; Frey-Wyssling, 1959). The pit membrane is flexible, and under certain conditions the torus occurs in a lateral position, appressed to one or the other pit aperture of the pit-pair (*aspirated* pit-pair; pl. 11*C*). The movements of the pit membranes and the changes in the position of the torus are reportedly influenced by pressure relations within the tracheids. Aspiration of pits that occurs in connection with heartwood formation is thought to be associated with the drying out of the central core of the wood and appearance of gases in nonconducting tracheids. The displacement of pit membranes seems to occur where a water-containing tracheid lies against one filled with gases (Harris, 1954). When the torus occurs in median position (pl. 11*B*), water passing through the bordered pit-pair presumably moves through the pores of the margo (Bailey, 1957*c*). If the torus is in lateral position, the movement of the water through the pit-pair is restricted. The torus is characteristic of the bordered pits in Gnetales and Coniferales, but may be poorly developed (pl. 13*D*). It is rare and sporadic in angiosperms.

In certain dicotyledons the pits of vessels develop minute outgrowths from the free surface of the secondary wall of the borders, which give the pits a sieve-like appearance. The processes are highly refractive, vary in number, shape, and size, and occur not only in the pit chambers but also on the inner surface of the secondary wall of vessels. In half-bordered pit-pairs they occur only in the bordered member of the pair. Bordered pits with such processes have been named *vestured pits* (Bailey, 1933).

The pits are variously arranged in different cells, and they are not spaced uniformly, even in a single cell. Moreover, they vary in structure within one cell. The distribution and structure of the pits within a cell depend much on the type of cells to which it is joined in a tissue. Simple pits may occur in all walls of a given cell or only in certain ones. A tracheary cell may have no pits in parts of walls joined to a fiber, large prominently bordered pits where it is connected to another tracheary cell, and much reduced borders where it is joined to a parenchyma cell. The pit-pairs between two pine tracheids have well-differentiated tori, but in the half-bordered pit-pairs which occur between tracheids and the parenchymatic members of the xylem tori are usually absent.

Pits may form definite patterns that have special names (Committee on Nomenclature, 1957). The bordered pits in tracheary cells show three main types of arrangement: scalariform, opposite, and alternate. If the pits are elongated or linear and form ladder-like series (fig. 3.5*A*), the arrangement is called *scalariform pitting* (from the Latin *scalaris*, pertaining to a ladder). Pits arranged in horizontal pairs or short horizontal rows characterize *opposite pitting* (fig. 3.5*B*). If such pits are crowded, their borders assume rectangular outlines in face view. When the pits occur in diagonal rows, the arrangement is *alternate pitting* (fig. 3.5*C*), and crowding gives the borders hexagonal outlines in face view. Small simple pits are often aggregated in clusters. Such an arrangement is called *sieve pitting*.



A *B* *C*

FIG. 3.5. Arrangement of bordered pits in vessel walls of angiosperms seen in face view. *A*, scalariform, *Magnolia; B*, opposite, *Liriodendron; C*, alternate, *Salix*. (All, ×375. After photomicrographs in S. J. Record, *Identification of the Timbers of Temperate North America*, John Wiley and Sons, 1934.)