sition and their microscopic [illegible]
walls is well illustrated by their permanent [illegible]
of growth of cells in volume (Heyn, 1940); elasticity, by the [illegible]
changes in volume in response to changes in turgor pressure (Frey-Wyssling, 1959). Notable tensile strength is characteristic of mechanical cells, particularly of the extraxylary fibers of monocotyledons and dicotyledons.

Some of the conspicuous differences in optical and other physical properties of walls are correlated with the orientation of the microfibrils. Thus, for example, walls or wall layers in which the microfibrils are oriented parallel to the long axis of the cell do not exhibit their anisotropy in transverse sections and do not contract longitudinally; on the contrary, walls having the microfibrils oriented at right angles to the long axis of the cell are strongly birefringent in transverse sections and contract longitudinally on drying (Bailey, 1954).

Because of its abundance in cell walls cellulose has a major influence upon their properties. Other substances add their properties or modify those imparted by the cellulose. Tensile strength is one of the remarkable characteristics of cellulose. Lignin, on the other hand, increases the resistance of walls to pressure and protects the cellulose fibrils from becoming creased (Frey-Wyssling, 1959).

FORMATION OF WALLS

Initiation of Wall during Cell Division

The process of somatic division of a protoplast into two daughter protoplasts may be separated into two stages: the division of the nucleus, or *mitosis* (*karyokinesis*), and the division of the extranuclear part of the protoplast, or *cytokinesis*. In cells having cell walls the new wall is formed during cytokinesis.

The divisions of the nucleus and the cell may follow each other so closely that mitosis and cytokinesis appear as one phenomenon; or the two may be separated in time. The ordinary somatic divisions, characterizing vegetative growth from the meristems, usually show a close correlation between nuclear and cellular divisions. In contrast, the two phenomena are widely separated in the formation of pollen and endosperm in many angiosperms, and in the development of the female gametophyte and the proembryo in gymnosperms.

The partition between the new protoplasts, when first evident, is referred to as the *cell plate*. If cytokinesis follows the nuclear division

immediately, the cell plate arises in the equatorial plane of a fibrous spindle, the *phragmoplast*, extending between the two groups of chromosomes that move apart during the anaphase of mitosis (pl. 4*E–G*). As these two groups develop into the telophase nuclei, the phragmoplast widens out in the equatorial plane and assumes the shape of a barrel. When the cell plate appears in the median part of the equatorial plane of the phragmoplast, the fibers of the phragmoplast disappear in this position but remain evident at the margins, until the cell plate appears here too.

If the diameter along which the cell is dividing is so short that the phragmoplast, after a slight widening, reaches the walls that are oriented perpendicularly to the plane of division, the phragmoplast appears to be connected to the two nuclei for the duration of cytokinesis. If, however, this diameter is longer than the original phragmoplast is wide, the phragmoplast extends laterally until it comes in contact with the cell walls, and during this extension it completely separates from the nuclei. As seen from the side, such a phragmoplast appears as two groups of fibers, disconnected from the nuclei but connected with each other by the cell plate, which follows the phragmoplast in its lateral extension (fig. 3.9*A*). In face views the phragmoplast has a somewhat varied appearance, depending on the shape and size of the dividing cells and also on the original position of the nucleus.

The progress of the phragmoplast and cell plate through the cell lumen is particularly striking in very long cells, for example, fusiform cambial cells, dividing longitudinally. The process of cell-plate formation in such cells is greatly extended in time and space and is clearly dissociated from the nuclear mitosis (Bailey, 1902*b*; chapter 6).

The phragmoplast and the mitotic spindle are proteinaceous in chemical structure (Olszewska, 1961*a*, *b*; Shimamura and Ota, 1956). The fibrous nature of the phragmoplast has been recognized in living material (Sitte, 1962) and in some electron micrographs (Sato, 1959); in others the phragmoplast was brought into relation to elements of the endoplasmic reticulum (Porter and Machado, 1960), or to the dictyosomes (Whaley and Mollenhauer, 1963), or to elements in the form of microtubules (Ledbetter and Porter, 1963). The phragmoplastic fibers appearing at the margins of the cell plate are sometimes called kinoplasmasomes, a term reflecting the old concept of the existence of a special kind of active, fibrous cytoplasm, the kinoplasm (Bailey, 1920*b*).

The views of cell-plate formation have been misinterpreted by some workers, and this, in turn, has led to misconceptions regarding the numbers of nuclei in ordinary somatic cells. The erroneous reports have been reviewed and corrected (Bailey, 1920*a*; Wareham, 1936).

Cytokinesis is not limited to meristematic cells with dense protoplasts.

Some of the meristematic cells themselves are highly vacuolated, and, furthermore, enlarging and prominently vacuolated cells of the ground tissue are known to divide actively during the growth of roots, shoots, leaves, and fruits of higher plants. In vacuolated cells the new cell plate eventually occurs in the region formerly occupied by the vacuole. One may observe, however, that during the early prophase of the nuclear division, that is, long before the beginning of cytokinesis, the nucleus comes to occupy a position corresponding to the future equatorial plate of the mitotic spindle and is surrounded by dense cytoplasm. A layer of this cytoplasm extends to the walls oriented at right angles to the future plane of division. It forms a cytoplasmic plate, for which Sinnott and Bloch (1941) coined the term *phragmosome*. The phragmosome forms a living medium in which the phragmoplast and the cell plate develop (fig. 3.8). Studies of this stage of division in the living state indicate that the amassing of cytoplasm around the nucleus before the formation of the phragmosome is associated with a cessation of the movement of particles in the streaming cytoplasm and an apparent increase in density of the cytoplasm (Jones et al., 1960). Reversion to free flow within the cytoplasm occurs only after the cytokinesis is completed.

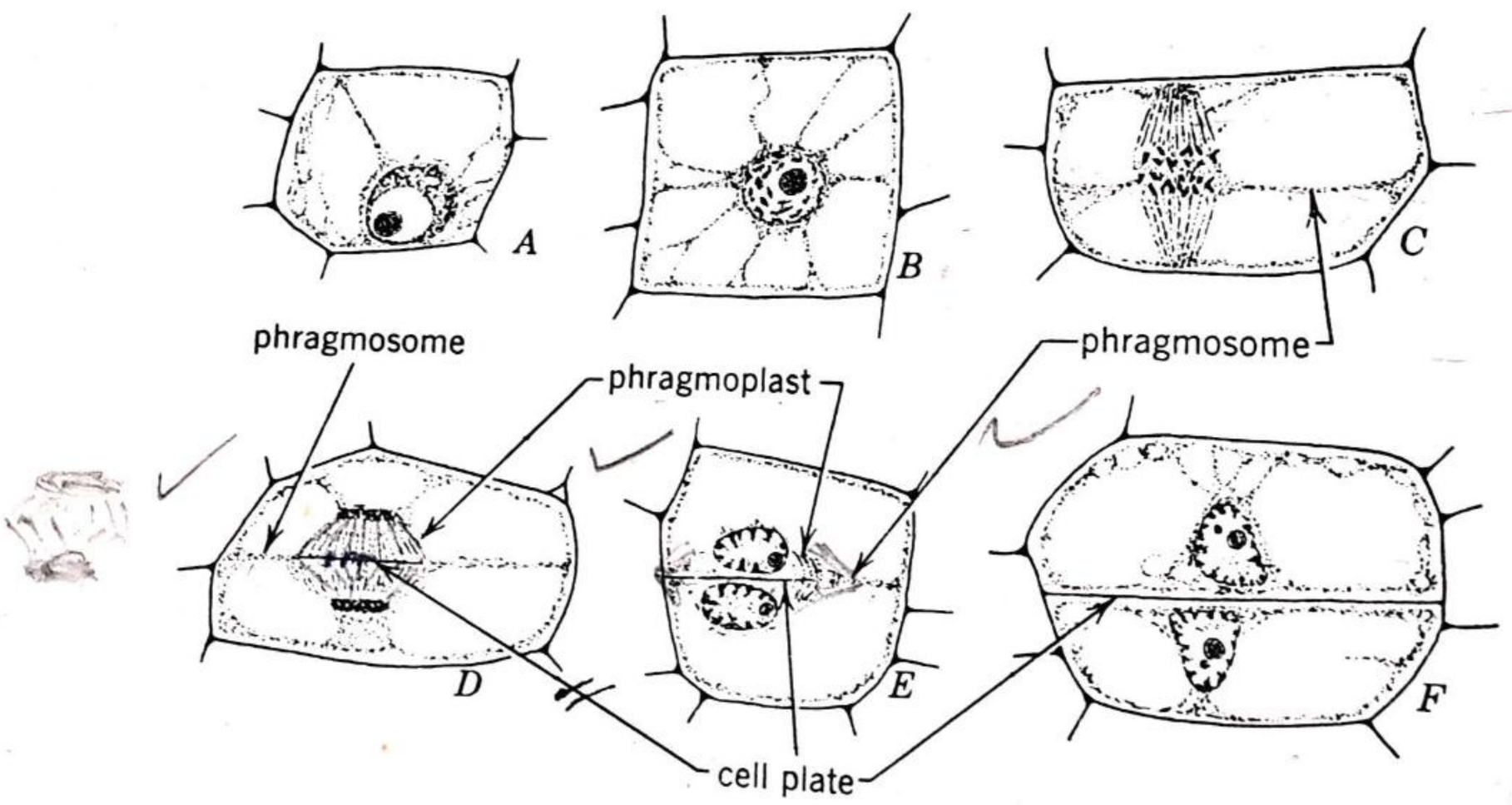

FIG. 3.8. Division of highly vacuolated cells in young pith of *Ligustrum*. *A*, cell in a non-dividing state. *B*, nucleus in prophase and located in middle of cell. *C*, nucleus in early anaphase; laterally, mitotic spindle is connected to parietal cytoplasm by a cytoplasmic layer, the phragmosome. *D*, daughter nuclei in telophase; barrel-shaped spindle between nuclei is the phragmoplast; cell plate appears in its equatorial plane. *E*, cell plate intersects one of the walls of mother cell. *F*, cell division is completed and cell plate occupies former position of phragmosome. (All, ×940.)

If a cell plate is not formed immediately after nuclear division, phragmoplasts may arise later. Sometimes no phragmoplast is formed; instead, the cell divides by a process called *furrowing*. Such division has been described in lower plants and in pollen and endosperm development in higher plants. It consists of the formation of cleavage furrows within the protoplast, starting at the existing walls and advancing inward until they meet and divide the protoplast into two or more cells. Cell-plate formation has been studied in living and fixed material and with light and electron microscopes (Becker, 1938; Porter and Machado, 1960; Sitte, 1962). It seems well substantiated that substances in semi-fluid state accumulate as vesicles—according to one view (Whaley and Mollenhauer, 1963), derived from dictyosomes—in the equatorial plane of the phragmoplast and cleave the protoplast in two (pl. 5*C*). The two new cytoplasmic surfaces become parts of the protoplasmic membranes (ectoplast, pl. 4*I*) of the two new cells. Pectic substances occur in the semifluid partition in the equatorial plane. These substances are regarded as forming the new middle lamella. A deposition of cellulose on both sides of this middle lamella, externally to the new protoplasmic membranes, is indicated by the appearance of double refraction, which becomes perceptible before the cell plate joins the walls of the dividing cell (Frey-Wyssling, 1959). Cellulose is deposited not only on the cell plate but around the entire daughter protoplasts (fig. 3.9*A–C*). Basically similar phenomena might be involved in cell division by furrowing.

Thus the partition that appears between the two sister protoplasts at cytokinesis undergoes different physical and chemical changes during the progress of cell division. There is no agreement regarding the stage of the process at which the visible partition should be called cell plate. The term has, therefore, no precise definition and merely serves, at present, as a designation for the first visible structure delimiting the two sister protoplasts from one another.

Growth of Walls

In considering the mechanism of wall growth it is necessary to differentiate between growth in surface area and growth in thickness. The former process is much more difficult to explain than the latter. Growth in thickness is particularly obvious in secondary walls but is common also in primary walls (as classified according to Kerr and Bailey, 1934). It occurs by a successive deposition of wall material, layer upon layer, that is, by a process known as *apposition*. But intercalation of new particles among those existing in the wall, that is, *intussusception*, is not necessarily excluded during thickening growth (Roelofsen, 1959).

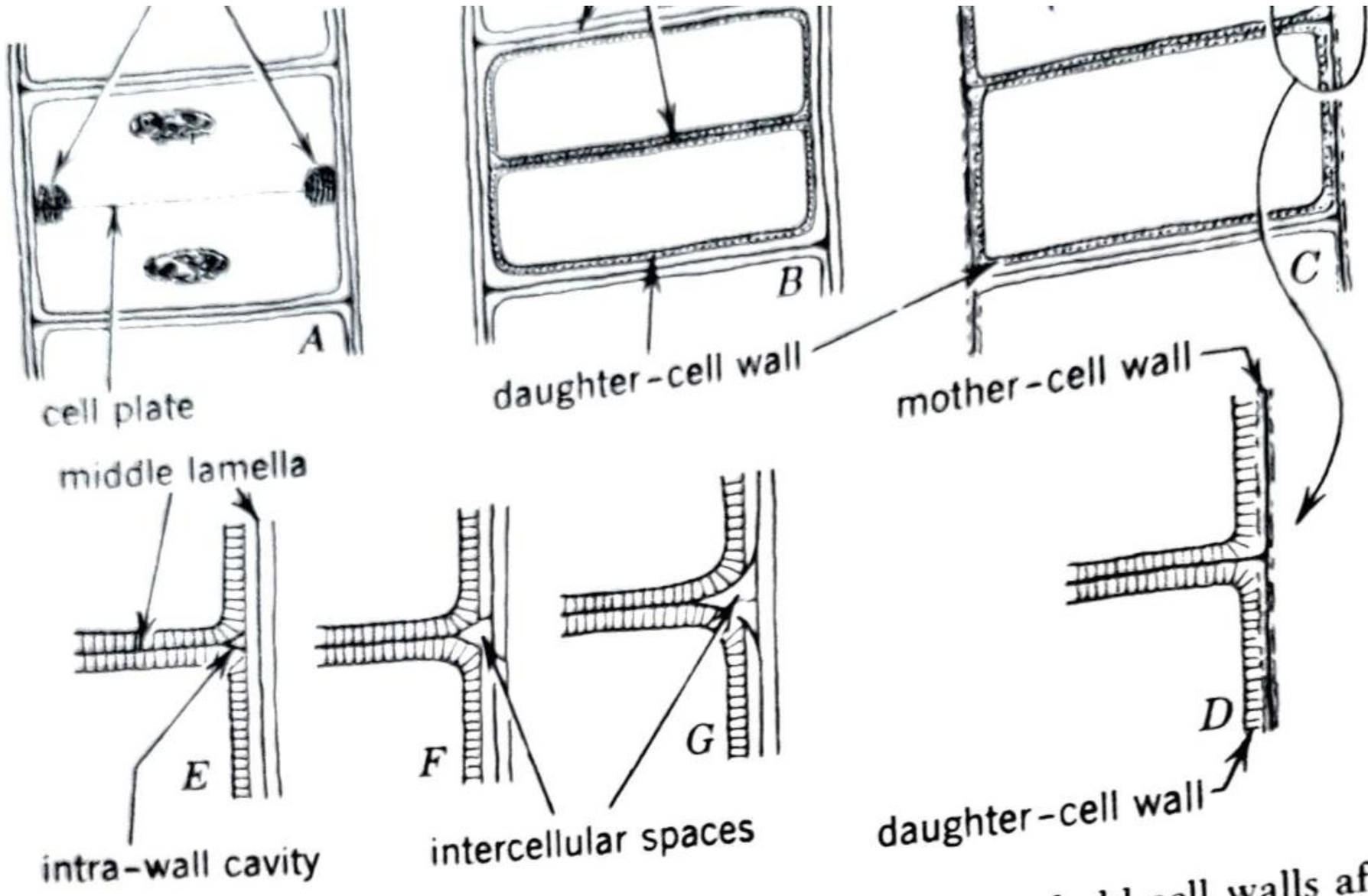

FIG. 3.9. Concepts regarding the adjustments between new and old cell walls after cell division. *A*, cell plate has been formed. *B*, two primary walls cemented by intercellular substance occupy the position of cell plate: primary daughter-cell walls have been laid down on the inside of primary mother-cell wall. *C*, *D*, daughter cells have expanded vertically and mother-cell wall has been stretched and ruptured opposite new wall. Thus, old and new intercellular lamellae have joined. *E–G*, establishment of continuity between old and new middle lamellae through formation of intercellular space. *E*, appearance of cavity between daughter- and mother-cell walls. *F*, dissolution of mother-cell wall next to cavity. *G*, completion of change of the intra-wall cavity into an intercellular space.

Growth of walls by apposition is usually centripetal. In other words it occurs from the outside and toward the lumen of the cell. Sometimes, however, wall growth has a centrifugal course, that is, in the direction away from the lumen. Centripetal growth is characteristic of cells forming tissues. Centrifugal growth is a specialized type of growth found in pollen grains and other spores. In such structures centrifugal growth is considered to be responsible for the formation of at least part of the exine (the outer wall). The more or less degenerated contents of the tapetal cells (chapter 18) surrounding the developing spores seem to be involved in the formation of exine (Roelofsen, 1959).

Many aspects are being considered with regard to the growth of cell walls in surface area. The question whether new material is being added to the wall during its extension is usually answered in the affirmative (Ray, 1962; Roelofsen, 1959; chapter 17). Despite the great increase in surface of the primary wall of enlarging cells, no appreciable decrease

in wall thickness is observable during such growth. Moreover, accurate determinations of the amount of cell-wall material in successive stages of growth reveal considerable increase of wall material per cell. Some of the exceptions of wall extension with only negligible addition of wall material were found in the growing staminal hairs of *Tradescantia* and staminal filaments of Gramineae. Another question concerns the growth of protoplasm in cells undergoing expansion. Apparently cell walls can increase in surface without a concomitant increase in protein nitrogen in the protoplast (Matthaei, 1957).

Investigators are concerned with the question whether growth of the wall in surface involves part of a given wall or the entire wall. In ground-parenchyma tissue growth occurs, as evidenced by the uniform increase of distances among the existing pit-fields, over the entire surface of a growing wall (Wilson, 1958, 1961; Ziegenspeck, 1953). Autoradiographic studies with labeled compounds also indicate incorporation of material over the total surface of parenchyma walls (Setterfield and Bayley, 1961). Certain types of cells, however, show localized growth, as, for example, fibers and tracheids (Wardrop, 1954), in which the tips grow intrusively among other cells (chapters 4, 6), and root hairs (Dawes and Bowler, 1959), in which typically growth in length occurs at the tips.

During the over-all extension of the primary wall the primary pit-fields are not only more widely spaced but they also enlarge in area and become subdivided by the deposition of microfibrils over the pit-field (Scott et al., 1956). As previously mentioned, plasmodesmata, too, may become subdivided (Krull, 1960). During cell division, however, completely new pit-fields are added (Wilson, 1958, 1961). Thus it appears that during growth the wall maintains a characteristic density of connections with contiguous cells.

The most complex aspect of the growth of wall in surface area is the growth of the cellulosic microfibrillar system. Electron microscopists have formulated several concepts of this growth (Wardrop, 1962). According to one, for example, synthesis of wall material occurs in localized regions scattered over the wall (*mosaic growth*), in which the cytoplasm pushes apart the existing microfibrils and weaves in new ones. A more widely accepted concept is that of the *multinet growth* pattern, which visualizes an apposition of successive layers of microfibrils, with the earlier layers becoming modified in microfibrillar orientation by wall extension during cell enlargement. The structure of many primary walls seems to support this concept.

The question whether primary walls grow predominantly by apposition or by intussusception has no unequivocal answer (Roelofsen, 1959), but

the preferred view is that appositional growth even though the microfibrils may be intertwined. On the other hand, some studies with radioactive isotopes suggest that new wall material may be deposited throughout the wall (Setterfield and Bayley, 1961). Moreover evidence has been presented (Matchett and Nance, 1962) that the distribution of isotope throughout the wall may be associated with a metabolic turnover of polysaccharides during their synthesis; that, in other words, the extension of the primary wall may be associated with a breakdown and resynthesis of the structural framework. This interpretation must be evaluated in relation to the concepts of mechanism of wall expansion, especially that considering the possibility of an increase in plasticity of the wall during growth (Setterfield and Bayley, 1961).

Studies with isotopically labeled substrates have indicated that intact glucose may be used directly in cellulose synthesis, but the mechanism of glucose polymerization has not yet been revealed (Setterfield and Bayley, 1961). It has been suggested that individual glucose residues are added to the tips of growing microfibrils and that this method of growth would explain the uniform thickness of microfibrils and absence of anastomoses.

Another complex aspect of wall growth has to do with the establishment of continuity between the new intercellular lamella and that located outside the primary wall of the mother cell. Workers visualize an extension and breakdown of the parent wall opposite the new middle lamella (fig. 3.9*A–D*; Priestley an Scott, 1939; Roelofsen, 1959). The formation of intercellular spaces might be associated with this phase of wall growth (fig. 3.9*E–G*; Martens, 1937, 1938).

FORMATION OF INTERCELLULAR SPACES

Although the cells in the meristematic tissues are generally closely packed, during tissue differentiation the close connection between walls of adjacent cells may be partly broken, with the appearance of intercellular spaces. The most common intercellular spaces result from a separation of cell walls from each other along more or less extended areas of their contact. These are the *schizogenous* intercellular spaces, so called because formerly the mechanism of their formation was thought to involve a splitting of the middle lamella (*schizo*, split; *genesis*, beginning; both from the Greek).

The origin of the schizogenous intercellular spaces is described as follows (Martens, 1937, 1938; Sifton, 1945, 1957; fig. 3.9*E–G*). When the new primary walls are formed between two sister protoplasts, the