11

Xylem

CONCEPT

The vascular system of the plant is composed of xylem, the principal water-conducting tissue, and phloem, the food-conducting tissue. As components of the vascular system xylem and phloem are called *vascular tissues.* Sometimes the two together are spoken of as the *vascular tissue.* The term *xylem* was introduced by Nägeli (1858) and is derived from the Greek *xylos,* meaning wood.

The physiologic and phylogenetic importance of the vascular system and its prominence among the structural elements of the plant body has led to a taxonomic segregation of plants having such a system into one group, the so-called *vascular plants,* or *Tracheophyta* (Cheadle, 1956). This group consists of the Psilopsida, Lycopsida, Sphenopsida, and Pteropsida (ferns, gymnosperms, and angiosperms).

The terms vascular plants and Tracheophyta refer to the characteristic elements of the xylem, the vessels and the tracheary elements in general. Because of its enduring rigid walls the xylem is more conspicuous than the phloem, is better preserved in fossils (pl. 29), and may be studied with greater ease. It is this tissue, therefore, rather than the phloem, that serves for the identification of vascular plants.

Structurally, the xylem is a complex tissue, for it consists of several different types of cells, living and nonliving. The most characteristic components are the tracheary elements, which conduct water. Some of the tracheary elements combine the function of conduction with that of support. The xylem also commonly contains specialized supporting elements, the fibers, and living parenchymatic cells concerned with various vital activities. Fibers may retain their protoplasts in the conducting xylem and thus combine vital functions, as starch storage, with the mechanical one of support. In certain groups of plants, the xylem includes laticifers. Sclereids differentiated from parenchymatic elements may be present.

The common association of fibers with other xylem and phloem elements brought about the introduction of the term "fibrovascular tissue" with reference to the xylem and the phloem. This term is rarely employed now.

CLASSIFICATION

The first xylem differentiates during the early ontogeny of a plant—in the embryo or the post-embryonic stage—and as the plant grows, new xylem continuously develops from the derivatives of the apical meristems. As a result of this growth, the primary plant body, which is eventually formed by the activity of the apical meristems, is permeated by a continuous xylem system (together with the accompanying phloem system) whose pattern varies in different kinds of plants. The xylem differentiating in the primary plant body is the *primary xylem*. The immediate precursor of this xylem is the *procambium* (chapter 4).

If the plant is of such a nature that, after the completion of primary growth, it forms secondary tissues through the activity of the *vascular cambium* (chapter 6), the xylem produced by this meristem constitutes the *secondary xylem* (pl. 28).

The histologic characteristics of the two kinds of xylem are given later in this chapter. Depending on the nature of the plant, the primary xylem is more or less distinct from the secondary, but in many respects the two kinds of xylem intergrade with each other (Esau, 1943). Therefore, to be useful the classification into primary and secondary xylem must be conceived broadly, relating the two components of the xylem tissue to the development of the plant as a whole, in a manner outlined in the preceding paragraphs and chapter 4.

ELEMENTS OF THE XYLEM

Tracheary Elements

Tracheids and Vessel Members. The term tracheary element is derived from "trachea," a name originally applied to certain primary xylem elements resembling insect tracheae (Esau, 1961). Two fundamental types of tracheary elements occur in the xylem, *tracheids* and *vessel members* (or *vessel elements;* figs. 11.1, 11.2*D–F*, 11.8, 11.9). In the mature state both are more or less elongated cells (some vessel members

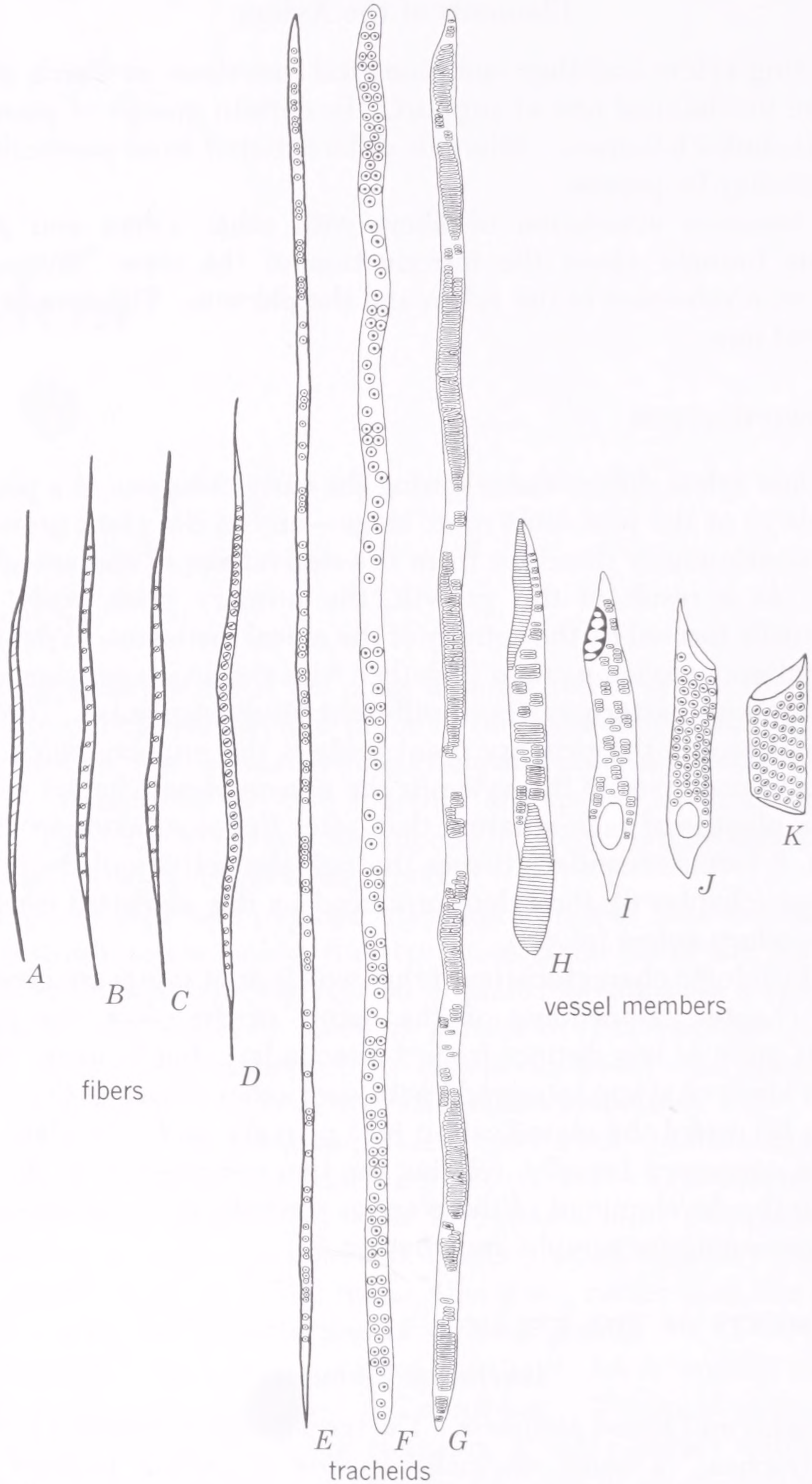

FIG. 11.1. Main lines of specialization of tracheary elements and fibers. *E–G*, long tracheids from primitive woods. (*G*, reduced in scale.) *E*, *F*, circular bordered pits; *G*, elongated bordered pits in scalariform arrangement. *D–A*, evolution of fibers: decrease in length, reduction in size of pit borders, and change in shape and size of pit apertures. *H–K*,

may be drum-shaped; fig. 11.9, pl. 36*A*) having lignified secondary walls and containing no protoplasts. They differ from each other in that the tracheids are imperforate cells having only pit-pairs on their common walls, whereas the vessel members are perforated in certain areas of union with other vessel members. Thus the vessel members are joined into long continuous tubes, the *vessels* (pl. 35*B*; sometimes called *tracheae*). Sap moving through these structures passes freely from element to element through the perforations, whereas in the tracheids it traverses the walls, particularly the thin pit membranes (Stamm, 1946).

The perforations of vessel members commonly occur on the end walls, but they may be present on the lateral walls too. The wall area bearing the perforation is called the *perforation plate* (Committee on Nomenclature, 1957). A perforation plate (fig. 11.2) may have a single perforation (*simple perforation plate*) or several (*multiple perforation plate*). The openings in a multiple perforation plate are arranged in a parallel series (*scalariform perforation plate*, from the Latin *scalaris*, ladder), or in a reticulate manner (*reticulate perforation plate*, from the Latin *rete*, net), or as a group of approximately circular holes (*ephedroid perforation plate*, as in *Ephedra*, fig. 11.8).

Each vessel (that is, a series of vessel members joined end to end) is limited in length, and the vessels in a series are connected to each other by imperforate walls in the same manner as tracheids. Water and aqueous solutions pass through these imperforate walls, but such substances as mercury and gases fail to do so. The exact length of vessels is difficult to determine. Some data suggest that individual vessels may be from 2 to 15 ft long, but in species with especially wide vessels in the early wood (ring-porous wood) the vessels appear to extend through the entire height of the tree (Greenidge, 1952; Handley, 1936).

Formation of a Vessel. A vessel originates ontogenetically from a longitudinal series of meristematic cells. These are procambial cells in the primary xylem, cambial derivatives in the secondary. The primordial vessel members may or may not elongate before they develop secondary walls, but they usually expand laterally (pl. 36*A*). After this growth is completed, secondary wall layers are deposited in a pattern characteristic for the given type of vessel element. The portions of the primary wall that later are perforated are not covered by secondary wall material. Nevertheless, they commonly become thicker, as compared

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evolution of vessel members: decrease in length, reduction in inclination of end walls, change from scalariform to simple perforation plates, and from opposite to alternate pit arrangement. (After Bailey and Tupper, *Amer. Acad. Arts and Sci. Proc.* 54, 1918.)