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CHAPTER XV

A SKETCH OF THE HISTORY OF PLANT ANATOMY

Among the various fields of present-day botany, anatomy is often considered to be largely of recent development. And such it is in certain aspects, especially those of the understanding of the morphology and phylogeny of both gross and minute features of structure, and those of knowledge of the detailed structure of complex tissues. Yet anatomy had its beginnings—beginnings as extensive and as important as those of taxonomy and morphology—in the studies of the Greeks in the last few centuries before Christ; and its foundations were laid in the seventeenth century, when it became more firmly established than taxonomy, morphology, or physiology.

The advanced position of anatomy in botanical science in the seventeenth century was, however, only temporarily maintained; during the following period of nearly two centuries progress was slow and vacillating. Meanwhile, taxonomy progressed through the important Linnaean period, and physiology through the times of Hales, Priestley, and others, to an equally important foundation. In anatomy, substantial progress began again in the middle of the nineteenth century, and at this time and during the decades immediately following, it perhaps may be said to have attained its maximum rate of development. Since this period there has been slow and steady progress, with somewhat more rapid development along certain lines in the past twenty-five or thirty-five years.

Throughout its progress, development in anatomy has been to a large extent dependent upon the stimulus of interest in some allied field. When paleobotany turned to interpretations based upon anatomy, the great impetus given to its own progress and to interest in phylogeny extended also to anatomy and vitally influenced the progress of this field of study. Advance in anatomy—after the first steps were taken in the sixteenth century and again in the early nineteenth century—has been, throughout, to a very large extent due to interest in comparative morphology. Only for brief periods has descriptive anatomy, as such, prevailed, and only rarely has descriptive or physiological anatomy contributed substantially to increased knowledge of the field. The fact that comparative morphology has dominated advance in anatomy has been of the greatest value in the laying of a solid foundation; study in this field has made clear the fact that only on such a basis can the most satisfactory progress be made. The most recent advances in anatomy have also been connected with the pursuit of phylogenetic studies. Anatomy is to an increasingly greater extent playing a part in the establishment of a natural system of classification—the goal toward which the efforts of morphological and taxonomic study are directed.

Anatomical study began in England, and since the days of Nehemiah Grew has continued almost without interruption in that country. During a large part of the nineteenth century the leading workers were in Germany and France; at the end of the century, however, the center of anatomical research passed back to England. The maintenance of interest in anatomy in England is doubtless due in large measure to the fact that early important studies were made there; to the development of paleobotany by the anatomical study of the wonderfully preserved flora of the English coal measures; and to the stimulus given to the study of the comparative anatomy of living forms by the study of the structure of ancient plants. It is, therefore, natural that English anatomists should direct their attention to comparative morphology and phylogeny. In Germany, the latter viewpoint has played an unimportant part; the numerous, important, and extensive studies made in that country have presented detailed structure with great accuracy, but are, as a whole, largely without correlation as to morphological or taxonomic meaning. Physiological plant anatomy has come almost wholly from Germany. In France, there has been a tendency toward broad morphological studies of a comparative nature, and these were numerous in the last quarter of the nineteenth century. In the United States anatomy has not at any time been a "popular field" of study; and only in the past thirty-five years has important research in this field been carried on here. Valuable results have come, however, from the restricted number of studies thus far made, throughout which the influence of the English viewpoint is dominant.

The Beginnings of Anatomy.—The interest of mankind in plants in a way that can be called truly scientific began, so far as we know, with the Greeks in the last centuries before the Christian era. Rudiments of the science of botany exist in the writings of the ancient Greeks of this time, but only in the books of Theophrastus of Eresus (about 369–262 B. C.) are distinctly botanical treatises found. Aristotle, the tutor and friend of Theophrastus, is known to have written extensively about plants, but these writings have been lost. The discussions of Theophrastus are philosophical in nature. His essays on structure deal with the kinds of organs, the relation of organ to organ, and of kind of organ to kind of organ. He distinguished in a tree, root, stem, branch, leaf, flower, fruit, and maintains that this is a normal sequence; he even recognizes roots, as such, when they are aërial. Thus he established the beginnings of descriptive morphology. These morphological studies he extended to gross internal features, to the anatomical structure of stems, roots, and leaves. He says: "Plants are made up of bark (*phloios*), wood (*zylon*), and pith (*metra*), when pith is present." Thus, two of the best-known and most-used anatomical terms, phloem and xylem, go back, in approximately their present form, to the very beginnings of anatomy; they are, indeed, classic terms. By the use of these distinctions Theophrastus describes in a rough way the gross differences in the stems of dicotyledons and monocotyledons, and even discusses the nature of annual rings.

Theophrastus describes the stem in more detail, as a fabric of veins, nerves, and flesh, not implying by these terms, however, homology with animal tissues. Veins and nerves are essentially one and the same, the nerves being the minute fiber-like parts, the veins the larger strands, apparently the vascular bundles. Veins and nerves are characterized by the fact that they can be split, but not otherwise readily separated; whereas flesh can be readily divided in all planes "like a lump of earth." Here is the beginning of the old anatomical classification of tissues—one to which at present occasional reference can still be found—as prosenchyma and parenchyma. Having distinguished the elements of the plant body, Theophrastus was able to state that wood is composed of nerves and moisture; pith, of flesh and sap; bark, of nerves, flesh, and sap. Here was made a real beginning of an acquaintance with the structure of plants. Thus did Theophrastus lay foundations in morphology and anatomy. At the same time he made important beginnings in classification, especially in nomenclature; many of our present-day generic names were first used by Theophrastus. For these reasons this Greek student of the third century before Christ has been called the father of botanical science. This may be said of him with especial significance as regards anatomy.

After the meager and crude, but still fundamental, contributions of Theophrastus to the science of botany, the interest of the Greeks in pure botany rapidly declined; and though botanical study was continued sporadically for a few centuries by them and by the Romans, it took the form of the application of botanical knowledge to medicine and agriculture. With the rise of the Christian doctrines, which stilled by their authoritative statements all inquiry into the origin and nature of living things, began the "Dark Ages" of biological science. For botany this period began to lighten only in the early part of the sixteenth century with the studies of the herbalists, and with the advances in classification made at the end of this and during the early part of the succeeding century. Throughout this period, which was one of progress in taxonomy alone, plant description was based on external morphology, since means of magnification were then unknown. Only by Valerius Cordus (1515–1544) and Andrea Caesalpino (1519–1603) were investigations of the internal structure of plants made. The former added brief descriptions of stem and petiole sections to his taxonomic descriptions, and the Italian botanist in his philosophical speculations made suggestions as to the anatomy of the plant which he gained in his search for its soul. Doubtless, Caesalpino's search was in large part theoretical, as he played a prominent part in starting the wave of interest in "idealistic" morphology which swept the field of morphological study during the next two centuries, and culminated in the philosophical morphology of Goethe and his followers. Though all Caesalpino wrote was obscured by Aristotelian philosophy, he appears to have made many good observations, and to have restarted botany on a basis of more exact terminology. Caesalpino postulated the presence of canals for conduction, and observed that many roots lacked pith. However, in the sixteenth century, nothing of moment was accomplished to break the long blank interval of nearly nineteen hundred years from the time of Theophrastus to the sudden awakening of anatomy in 1671.

The Discovery of the Cell.—In the middle of the seventeenth century a new field of botanical research was abruptly established by the use of lenses to determine details of internal structure. Curiosity as to the minute structure of plants led quickly to the rise of anatomy. One of the first of the investigators who examined all sorts of things with the "new toy," the magnifying lens, "to see what they were like" was the Englishman, Robert Hooke (1635–1703). Hooke, more or less incidentally—he was a mathematician and an architect, and not in any way actually interested in plants—found in connection with his examination of various things under the lens that plant tissues are made up of units which he termed "cells." He found that cork and charcoal, as well as other tissues, are "perforated and porous, much like a honeycomb." To the cavities of such honeycomb-like structures Hooke applied the term *cell*. The walls were *interstitia*, and not parts of the cell in his interpretation. Not until the beginning of the nineteenth century was it recognized that a part of the interstitial substance is definitely related to each cavity. Hooke published his discovery of plant cells in 1665 in his *Micrographica*, together with descriptions of many other structures seen through the lens. Thus it was a microscopist—for Hooke cannot be considered a botanist—who made a discovery of the greatest importance to the science of botany.

The Founders of Plant Anatomy.—The immediate value of Hooke's researches, however, was the stimulus they imparted to studies of plant structure. These studies bore fruit in the foundation works of Marcello Malpighi (1628-1694) and Nehemiah Grew (1641-1712), which appeared in the years immediately following. The suggestions of Hooke led to the systematic study of plant tissues by Grew, an English physician, and by Malpighi, an Italian physician and university professor. These men, working independently, each knowing nothing of the studies of the other, presented at the same time monographs on the structure of plants which stood for a century as the standard works in this field. Both men approached the study of plants from the standpoint of medicine, hoping to find in plants structural conditions comparable with those in animals. Grew studied plant structure for several years before presenting "The Anatomy of Vegetables Begun," which was published by the Royal Society in 1672, and presented in print at the very time when the Society received Malpighi's manuscript dealing with the same subject. There seems to be no question but that the work of Grew deserves priority, though the papers of both men were received by the Society at the same time; nor is there any question but that the work of each was wholly independent of that of the other. In their later studies, however, each

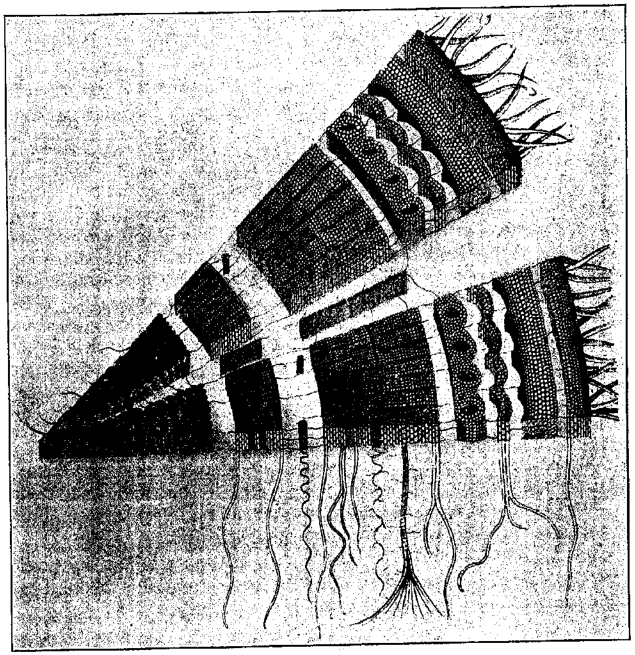

FIG. 143.—"Sumach Branch, cut transversely . . . with several breaks to shew ye Contexture both of ye Perpendicular & Horizontal Fibers." (*The Anatomy of Plants*, Nehemiah Grew, 1682.)

owed much of suggestion and information to the other. Grew's first publication was morphological, largely, rather than anatomical; it was followed by three others, more strictly anatomical in nature, the final treatise, published in 1682, being "The Anatomy of Plants, With an Idea of Philosophical History of Plants, and Several Other Lectures, Read before the Royal Society." In these four papers Grew discusses the grosser structure of plants, contrasting the vascular skeleton with that of animals, and describes the finer structure in much detail. This seems to have been done with infinite care and great skill. His detail does not to any great extent reach to the description of the cell itself, but deals largely with the manner in which tissues are built up of cells. He thought of the tissue of plants as a complex web of fine threads (Fig. 143):

> The most unfeigned and proper assemblance we can at present make of the whole *Body* of a *Plant*, is, To a piece of fine *Bone-Lace*, when the women are working it upon the *Cushion;* For the *Pith*, *Insertions* [rays], and *Parenchyma* of the *Barque*, are all extream Fine and Perfect Lace-work; the *Fibers* of the *Pith* running *Horizontally*, as do the *Threds* in a Piece of *Lace;* and bounding the several *Bladders* of the *Pith* and *Barque*, as the *Threds* do the several *Holes* of the *Lace;* and making up the *Insertions* without Bladders, or with very small ones, as the same *Threds* likewise do the *Close* Parts of the *Lace*, which they call the *Cloth-Work*. And lastly, both the *Lignous* and *Aer-vessels*, stand all *Perpendicular*, and so cross to the *Horizontal Fibers* of all the said *Parenchymatous* Parts; even as in a Piece of *Lace* upon the *Cushion*, the Pins do to the *Threds*. The *Pins* being also conceived to be *Tubular*, and prolonged to any length; and the same Lace-work to be wrought many *Thousands* of times over and over again, to any thickness or hight, according to the hight of a *Plant;* and the *general composure*, not only of a *Branch*, but of all other *Parts* from the *Seed* to the *Seed*.

Thus Grew recognized, in a way, vertical and horizontal systems, and the constancy of these conditions throughout the plant.

Grew presents a classification of plant tissues, which in its crude separation of prosenchyma from parenchyma is essentially the same as the classification of Theophrastus. In his own words:

> All the *Parts* of a *Vegetable*, the *Root*, *Trunk*, *Branch*, *Leaf*, *Flower*, *Fruit*, and *Seed*, are still made up of *Two* substantially different *Bodies* . . . All properly *Woody Parts*, *Strings* and *Fibers* are *One Body:* All simple *Barques*, *Piths*, *Parenchymas* and *Pulps* . . . all but *One Body*, the several *Parts* of a *Vegetable* all differing from each other, only by the various *Proportions* and *Mixtures*, and variated *Pores* and *Structure* of these *Two* Bodies.

It is apparent that Grew understood the method of secondary growth. This takes place, he says,

> . . . betwixt the *Wood* and *Barque* . . . every year the *Barque* of a *Tree* is divided into Two Parts, and distributed two *contrary* ways. The outer Part falleth off toward the *Skin;* and at length becomes the *Skin* it self . . . The inmost portion of the *Barque* is annually distributed and added to the Wood; . . . So that a *Ring* of *Lymphaeducts* in the Barque this year, will be a *Ring* of *Wood* the next; and so another Ring of *Lymphaeducts* and of *Wood*, successively, from year to year.

An important structural condition seen by Grew is the fact that the xylem in the roots is radially arranged, and that the vascular tissue of roots forms a solid core and that of stems a hollow cylinder. In plants, Grew looked for vessels like those of animals, and found them in spiral vessels—already discovered by Malpighi—which he describes with precision. However he knew only the "fine narrow Ribband, woun'd spirally, and Edg to Edg;" the primary wall was not seen. He could see and understand parenchyma better than other tissues. Parenchyma to him was "an infinite Mass of little *Cells* or *Bladders*. The sides of none of them, are Visibly bounded within itself. So that the *Parenchyma* of the *Barque*, is much the same thing, as to its conformation, which the Froth of *Beer* or *Eggs* is, as a fluid . . . ."

The terms "parenchyma" and "vessel" thus go back to Grew in much the sense of present-day use. Other terms, such as "cuticle" and "cortex," apparently first used by him, have today different values.

There are evidences in a personally annotated copy of "The Anatomy" that Grew after the publication of his papers also studied the ontogeny of tissues; in his notes he observes: "Air-vessels of Parenchyma, transformed, as Caterpillars to Flys."[1]

Grew's work was colored by the philosophical tendencies of the time, but to a surprisingly small extent. In his mild manner, he protests against the growing idealistic conception that it is "according to the *idea* of the philosophers that things are so and so, no matter what the actual condition is."

> "Grew believed that the 'Outward Elegancies of *Plants*' might be for the purpose of giving delight to the human race, but he was the first to point out that as the 'Inward Ones, which, generally, are as Precise and Various as the Outward,' are so seldom seen, their purpose can hardly be for this, but must be for the benefit of the plants themselves, 'That the *Corn* might grow, *so;* and the *Flower*, *so*, whether or no Men had a mind, leisure, or ability to understand *how*.'"[2]

This was a strong statement at a time when it was believed that the purpose of the entire organic world was but to serve mankind, when it was held by some that even the fossils in the rocks were divinely created ornamentations of the interior of the earth for the pleasure of man whensoever he might happen upon them. Grew was, indeed, a man before his time, and well deserves the title of "founder of plant anatomy."

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[1] "Makers of British Botany," p. 52.

[2] "Makers of British Botany," p. 64.

Malpighi's work covered much the same ground as that of Grew, and his conceptions were much like those of his fellow worker, but were even less affected by philosophical considerations. In his generalizations he was, however, less acute and less thorough than the English anatomist. Like Grew, Malpighi believed wood to be derived from the inner bark by transformation, an opinion very closely correct, as can readily be understood. Credit should be given Malpighi for the discovery of spiral vessels—a discovery which Grew later expanded—and for the discovery of stomata. Like Grew, he speaks freely of tissues as made up of bladders, utricles, and fibers, but he did not understand these to be cells as they are thought of today. He saw tyloses and illustrated them, but quite naturally, did not distinguish them from other "bladders." Many of the terms used by Grew were taken up by Malpighi. The latter, himself, established few terms; his Latin term *liber* for the fibrous elements disposed in sheets in the inner "cortex" persisted for a very long time, only gradually to be replaced by the Anglo-Saxon *bast*.

Both Grew and Malpighi related their anatomical discoveries to function, and carried physiological investigations to a stage in many ways comparable with that reached in their studies of structure. On this account they have been called physiological anatomists. Grew dealt especially with function as related to structure in his investigations of the movements of sap. Both of these investigators also made morphological studies of flowers, leaves, and roots.

The Eighteenth Century.—After the death of Grew, interest in plant anatomy waned in England, but rose slowly on the continent of Europe, where increasing numbers of students took up this field, attracted doubtless by the opportunities presented by the constantly improved microscope. Through the eighteenth century the errors and misconceptions of the two anatomists of the preceding century were gradually removed, but only too often were replaced by others equally bad or even worse. The prevalent idea that all vessels were spiral was banished by the Dutch student, Antony van Leeuwenhoek (1632–1723), who first described pitted vessels. The study of the growing layer of the "inner Rind," begun by Grew and Malpighi, was continued by the French arboriculturist, Du Hamel (1700–1781), who gave the term *cambium* to "a gelatinous generative zone in the inner cortex." In Germany, Caspar Friedrich Wolff (1733–1794) studied plants persistently under the influence of the idealistic morphology which was then at its height. Wolff's theory that a tissue is a homogeneous matrix "filled with bubbles, as is rising dough," stimulated research in the nature of tissue, and this research became productive of most important results in the early part of the next century. The eighteenth century was a period of slight progress in all fields of botany with the exception of taxonomy; descriptive morphology made but little advance, and "internal morphology," anatomy, but little more. During the entire century no advance of importance was made in anatomy, and no work replaced that of Malpighi and Grew until well into the nineteenth century.

The Nineteenth Century.—In France, anatomy was founded by Charles Francois Mirbel (1776–1854), who elaborated Wolff's theory, stating that new cells appear in a homogeneous matrix as cavities which have openings into one another for the passage of sap. Mirbel was vigorously opposed in his theory of tissue structure and of cell origin by Kurt Sprengel (1766–1833); and, though the controversy in which they became involved produced little result in the way of new or more accurate information as to the nature and origin of the cavities known as cells, it brought anatomy again into prominence. Sprengel agreed with Mirbel that cells opened into one another, but stated that new cells arise within the contents of old cells as small vesicles which become enlarged by absorption of water. (These "vesicles" were probably starch grains.) In this theory Sprengel was supported for many years by Ludolph Christian Treviranus (1779-1864). Treviranus, while studying growing tissues, made the important discovery that vessels were formed from series of cells by the disappearance of cross-walls. (Grew had not understood the transformation, and had not published his observations on vessel formation.) Treviranus also first saw the development of the spiral band in protoxylem cells.

The study of cell ontogeny thus initiated by Treviranus was continued by Johann Jakob Bernhardi (1774-1850), who was a more accurate observer and more original in his methods of study. He discovered annular elements, and recognized that in them and in spiral cells the thickened rings and bands were tied together by a primary wall. He noted that this type of cell does not occur in secondary wood. He stated that a spiral vessel never changes its nature as claimed by the metamorphosists, who—at this time at the height of the influence of fanciful conceptions—extended their philosophy to cover all parts of the plant.

The discussions of Mirbel, Sprengel, and others concerning the origin of these cavities naturally led to further study of the matrix in which they lay, the "interstitia" of Hooke. In the study of these, Johann Jakob Paul Moldenhawer (1766–1827) introduced the new method of maceration, and, by means of this, at once demonstrated that each "cell" had a wall of its own, and that the cavities were, therefore, separated by two walls, not one. Thus was banished the view of Wolff, Mirbel, and others that the cells were like bubbles in a structureless matrix. Moldenhawer called attention to the union of fibers, vessels, and parenchyma in definite strands and gave to such masses the term *fibrovascular bundle*, a term which is only now being supplanted by the better form, *vascular bundle*.

It is evident that Moldenhawer saw clearly the compound nature of the bundle, and this conception enabled him to look upon the stem of a dicotyledon as made up of vascular bundles which gradually fuse to form a woody cylinder, another morphologically incorrect idea which has persisted to the present day.

The discovery of the individuality of the cell wall stimulated the study of this structure, and a long controversy arose as to its origin and nature. In the study of the cell, the cell cavity yielded the position of importance to the cell wall, which now became "the cell," the contents of the cavity being thought of merely as "cell contents" or "nutrient sap." Interest in the latter was thus, for the time being, subordinate, though it came to the front briefly in 1831 through the "discovery" of the nucleus by Robert Brown (1773–1858). The nucleus, however, had been noted by others before, though no suggestions as to its probable importance had been made.

FIG. 144.—Hugo von Mohl (1805–1872).

The controversy over the origin and nature of the cell wall naturally involved the origin of cells themselves, and the first suggestions of cell division, as distinct from free cell formation, seem to have been made by Franz Julius Ferdinand Meyen (1804–1840). Meyen, however, did not carry his investigations of cell division very far. His interest lay not in studying structure, but in writing about it. Further, his observations were, unfortunately, inaccurate. He stated that there were only three kinds of "tissue organs"—cells, spiral tubes, and sap vessels; in this statement he neglected the discoveries of Treviranus that vessels consist of fused cells, and went back for the basis of most of his statements to the opinions of older writers.

The attention given to the cell wall was, however, soon replaced by the rapidly increasing interest in the "cell contents." To students of cellular structure it became increasingly evident that the most important part of the cell was this "contents," from which attention had been temporarily turned away. This opinion was first strongly expressed by Hugo von Mohl (1805–1872—Fig. 144), who emphasized the fact that the contents were "living," and named the vacuolated body the *primordial utricle*. Von Mohl, in his earlier work, was prejudiced by the views of the older anatomists, and doubtless drew the term "utricle" from them. The great structural and functional importance of the "primordial utricle" soon became apparent, and, though the term was an unfortunate one in several ways, it persisted for a long time. Von Mohl stated that the utricle was made up of *protoplasm*, a term which was already in use by zoölogists for the contents of animal eggs. With the recognition of the fundamental nature of the protoplast, thus initiated by von Mohl, the use of the term "cell" became more or less fixed in the sense of protoplast; and this interpretation of the term—the wall being merely a limiting or protecting secretion of the cell, and not a part of the living cell—has persisted largely to the present day. Occasional efforts have been made to demonstrate that the wall is definitely a part of the living cell, that is, that it is composed, at least in part, of living material. In this question of the possibly partly protoplasmic nature of the wall of living cells there seems to be at present renewed interest. An answer to the question would definitely end the vacillation in the meaning of the term "cell" between lumen, wall, protoplast, and protoplast plus wall, which began with Hooke and continues today.

The Cell Theory.—The great stimulus given to the study of cell contents by the discovery of the similarity of "protoplasm" in animal and plant cells, added to the ever-increasing information as to the omnipresence of cells, soon resulted in the beginning of a theory of the structure of organic bodies. This foundation was laid by Matthias Jacob Schleiden (1804–1881) and Theodor Schwann (1810–1882), who worked on plant and animal tissues, respectively. Independently, they became acquainted with the structure of cells.

When the information each had acquired was brought together—in personal discussion and laboratory study, so the story goes—they became of the opinion that cells are fundamentally alike throughout the plant and animal worlds. As a result of this decision, each produced in 1838 a treatise on the subject, that of Schwann, which he himself termed "The Cell Theory," being the more comprehensive. Schwann says:

> The elementary parts of all tissues are formed of cells in an analogous, though very diversified, manner, so that it may be asserted *that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells* . . . The development of the proposition that there exists one general principle for the formation of all organic productions, and that this principle is the formation of cells, as well as the conclusions which may be drawn from this proposition, may be comprised under the term *Cell Theory*.

Both Schleiden and Schwann were thus concerned in the proposal of the theory that the body of organisms is composed of cells and cell products. The tremendous importance of this to the science of biology was at once recognized by students in both fields. In botany, interest was turned abruptly from the study of vascular anatomy and the ontogeny of tissues to the new field. Immediately, controversies arose over the method of cell formation, the rôle of the nucleus, the nature of protoplasm, and over other similar problems which are now looked upon as cytological, and with which, therefore, the present sketch need not deal.

In the years just preceding the presentation of the cell theory, the first studies of the structure of fossil plants—by Cotta in 1832 and Witham in 1833—began to stimulate the development of anatomy. Thus, very early began the contributions of paleobotany to anatomy, contributions which have been of the greatest importance in the development of the subject. Indeed, woody plants soon became better known anatomically in a fossil than in a living state. The influence of the study of the internal structure of fossil plants upon anatomy has continued to the present; it was doubtless greatest in the last third of the century when paleobotany and phylogeny advanced rapidly. The attempts to establish the identity and the relationships of fossil plants led naturally to an emphasis on comparative morphology and phylogeny. And, since external morphological features were often lacking, or considered to be of little value, attention turned to internal structure. Anatomy was forced to progress in order that it might fulfil the demands made upon it for explanation of the structure of fossil plants. Compared with paleobotany, taxonomy and physiology have had little effect upon the progress of anatomy.

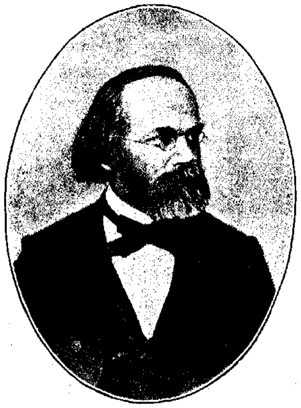
FIG. 145.—Carl von Nägeli (1817–1891).

The period during which the cell theory appeared, the second quarter of the nineteenth century, was one of great activity in anatomical research. Among other fields of botany, only in morphology and taxonomy can it be said that comparable progress was made. The great advances made were due largely to the work of von Mohl and Carl Wilhelm von Nägeli (1817–1891—Fig. 145). Both of these men were turned from the immediate fields of their research—histological studies—to enter the all-absorbing discussion of the cell theory, and contributed to its elaboration in important ways; both later returned, however, to the study of tissues and cell structure. Von Mohl was an unprejudiced investigator, thorough and accurate in the details of his work, and unhampered by philosophical considerations or by the physiological conceptions of the day. His first work of importance concerned cell ontogeny, in which he demonstrated the progressive thickening of the wall and the relation of secondary to primary layers, disposing finally of the old "transformation" views, such as, that the spiral vessel gave rise by metamorphosis to all other types. Von Mohl's painstaking and accurate observations put an end definitely to the two-century-long, fanciful philosophy of metamorphosis, and of idealistic morphology. In connection with wall development, von Mohl learned that pits are thin places in the wall and not pores or projections; also that the "intercellular substance" was the primary wall. Out of his studies of cell-wall development grew his theory of wall thickening by apposition.

Von Mohl's contributions to anatomy are numerous and most varied. He determined the nature and method of formation of vessels. He described the structure of the epidermis and demonstrated the nature of the cuticle; also the nature of lenticels and of cork, and the consequent formation of "bark" with its constant loss and renewal. Some of these tissue descriptions had, however, been outlined by Grew. Von Mohl first traced the course of bundles, both in monocotyledons and in dicotyledons, and confirmed their complex nature; in the ontogeny of the stem he showed that the first bundles of the stem were bundles connecting with the leaves.

In von Mohl's work we have for the first time accuracy of observation and of statement; with it opens a new epoch in plant anatomy. So excellent was von Mohl's work that much of it stands unquestioned today.

A classification of tissues was made by Franz Unger (1800–1870), but this was wholly empirical and had no morphological basis whatever. As a classification it was not followed to any extent, chiefly because a much better one soon appeared in the work of Nägeli. Unger's classification was, however, the best that had been proposed up to that time. Unger took part in the discussions of the cell theory, entered the controversy as to the method of cell origin, and contributed to the ontogenetic studies so popular at that time. However, it is chiefly Unger's textbook of anatomy and physiology, one of the first good texts in these fields, which brings this most versatile botanist into the field of anatomy, for Unger's major endeavors lay in pathology and paleobotany.

The study of vascular bundles led Hermann Schacht (1824–1864) to claim that the separate bundles of an axis arose by the "branching" of solid cylinders. At the time this was considered absurd, and distinctly a retrograde step in anatomy; and as such it has continued to be looked upon until very recently. However, Schacht was not, of course, thinking of the phylogenetic development of bundles and steles.

Theodor Hartig (1805–1880), a keen observer, who worked chiefly on wood and phloem, discovered the sieve tube and claimed that it was perforated. Von Mohl disputed the fact of its perforation, but Nägeli later substantiated Hartig's claim.

Nägeli's attention, like von Mohl's, was largely centered on ontogeny. He studied apical meristems particularly, and traced the segments of the meristem from apical cells and apical meristems to mature tissues and organs. From this he passed naturally to the study of the development of vascular bundles from procambial strands. He classified tissues as *generative* and *permanent*, dividing each of these into parenchymatous and prosenchymatous types. To prosenchymatous generative tissues he applied the term "cambium," a term which had been used earlier by Du Hamel, but in the very loose sense of a structureless matrix in which cells arose. Nägeli distinguished between primary and secondary meristems, and introduced the theory of wall thickening by intussusception. He studied sieve tubes in secondary phloem and put forward essentially the theory of their function that is chiefly held today—that they serve for conduction of the less diffusible plastic materials. In the study of vascular bundles he distinguished between cauline, common, and foliar strands. To the parts of the bundle he applied the terms "xylem" and "phloem," not understanding, however, a difference of function in the two parts. Nägeli is commonly looked upon as the originator of the terms "xylem" and "phloem," and for their present form he does appear to be responsible. However, Theophrastus had already used them in slightly different form, though in much the same sense.

Though von Mohl avoided generalizations to a fault, Nägeli made most comprehensive studies, and drew definitely clear conclusions from his numerous data. The clarity and usefulness of von Mohl's and Nägeli's classifications and conclusions are due to the morphological basis which they adopted for their studies. Through this, many obscure points in the older anatomy were readily cleared up. With the work of von Mohl and Nägeli, anatomy begins to resemble in its terms and in its methods the anatomy of today. It may well be said that the modern epoch was ushered in by these two men.

Grew and Malpighi laid a substantial foundation for the science of plant anatomy; Nägeli and von Mohl built its superstructure. More recent workers have determined the principles of construction and elaborated the superstructure, adding details, but have modified the framework only in minor ways.

The Modern Period.—Following the establishment of the cell theory, and of a substantial understanding of cell division, of meristem development, and of fundamental vascular bundle structure, attention centered for some time on the meristems, especially on the cambium, and upon the origin and structure of secondary tissues, particularly xylem and periderm. The acquisition of correct information in these fields was largely due to the efforts of Carl Sanio (1832–1891), a Prussian school teacher.

Sanio established the place and the method of origin of the cambium, and studied the activities of this meristem as related to the formation of annual rings. He worked extensively also on the structure of wood, accurately describing gymnosperm wood in remarkable detail considering the microscopes available to him. Bars of Sanio and trabeculae were first described by him, and bordered pits, the general nature of which had already been learned by Schacht, were also described in accurate detail. He extended his studies of the ontogeny of the secondary tissues to the periderm, the development of which he followed through. Sanio is perhaps best known for his studies in the comparative anatomy of gymnosperm and dicotyledon stems, in which studies he placed emphasis on the elements of the wood, their structure and distribution. The details of wood structure thus first accurately portrayed, together with his discovery of the procambial "thickening ring," constitute probably his most important contributions. Though the nature of secondary growth and of the annual ring had long been known in a general way, the ontogenetic beginnings of such growth were wholly obscure. These Sanio presented definitely, demonstrating place and method of origin of primary bundles and the relation of the cambium to these strands.

Sanio was one of the most prominent anatomists of his time, in method and viewpoint resembling Nägeli. With Nägeli and von Mohl, he should be associated as one of the founders of modern anatomy, and in this respect he is deserving of more credit than is commonly given him. His work surpassed that of Nägeli in accuracy and, in some respects, in importance, as did Nägeli's that of von Mohl.

Sanio's study of meristem development led Johannes von Hanstein (1822–1880), who had been working along lines similar to those followed by Sanio and Nägeli, into the same field. Hanstein showed the origin of Sanio's "thickening ring," by distinguishing in root and stem tips three definite histogenic layers which give rise to epidermis, cortex, and vascular cylinder. To these "histogens" he gave the names *dermatogen*, *periblem*, and *plerome*, respectively. Under the sway of the strong morphological tendencies of the time, Hanstein ascribed to these three layers definite morphological value, and believed them constant in value and in occurrence. Over this opinion controversy quickly arose. Though De Bary soon showed that the theory could not be applied universally and that the histogens lacked morphological value, the controversy continued until the end of the century, and even today Hanstein's histogens are commonly believed to be of characteristic and constant occurrence.

Heinrich Anton De Bary (1831–1888), a student primarily of the fungi, brought together in 1877 the knowledge of anatomy up to that date, publishing at that time his extensive "Comparative Anatomy of the

Phanerogams and Ferns." This book presents the enormous amount of information available at that time, arranged in a way which can only be said to be De Bary's own, and established a reasonable and workable terminology. The content of the book is arranged with little logical sequence; the treatment gives little idea of morphological and still less of physiological distinction; and from it can hardly be readily obtained a comprehensive understanding of the general structure of a plant. Yet so critically have the facts been judged and so accurately and completely have they been presented that De Bary's textbook is of the greatest value and has been the most generally useful and usable reference book in plant anatomy during the nearly fifty years since its appearance. Today it still stands an excellent reference text, the most valuable of all such books.

Physiological Anatomy.—As it became increasingly evident that Hanstein's close-drawn lines of morphological tissue classification based on ontogeny were of little value, a new basis for anatomical description and classification was sought. This basis was found in function by Julius von Sachs (1832–1897), who made the first physiological classification. Epidermal, fibrovascular, and fundamental tissues derived from a uniform meristem were suggested by him as the basic types. The epidermal tissues included all outer protective tissues; the fibrovascular, all actually conducting cells; the fundamental was a catch-all for whatever did not fall into the other two groups, such as medullary rays, the pith, the cortex. This classification met with opposition on the part of anatomists, for whom De Bary expressed the general feeling in his views that, though Hanstein's system could not be rigidly applied, only a classification based on development could be most satisfactory and most useful.

The physiological viewpoint of anatomy, thus begun, became more prominent in the work of Simon Schwendener (1829–1919). The classification of tissues on a physiological basis was extended by Schwendener's researches and has reached high development in the work of Gottlieb Haberlandt, now professor of plant physiology at the University of Berlin. The latter has worked out in detail a complete physiological plant anatomy, presented in his textbook, "Physiologische Pflanzenanatomie," which has appeared in several editions from 1884 to 1918. In this book the physiological viewpoint dominates all structural description; purely morphological classifications or arrangements are disregarded. Tissues are grouped according to function, constituting systems called dermal, absorbing, conducting, storage, aërating, sensory, etc. In such classification a tissue is not necessarily structurally continuous, the cells forming a given tissue being perhaps distributed through various parts of the plant body, as, for example, in the case of conducting tissue, where, in the morphologist's "xylem," only the vessels, tracheids, and parenchyma form the conducting tissue; fibers and fiber tracheids belong to the mechanical system. Thus, in many kinds of wood, such as that of *Acer*, what to the morphologist is xylem contains scattered through it only a rather small proportion of the physiologist's xylem. In similar ways terms are used in senses wholly physiological except for occasional cases when the basis is said to be "topographical." Whether physiological anatomists desire to supplant morphological conceptions may perhaps be questioned; they have, however, developed the structural material in such a way that it is useful chiefly to the physiologist. In the establishment of these conceptions, a considerable element of confusion has been added to the already confused state of anatomical terminology, since new terms have not been coined to any extent by physiologists, but those already in use have been applied in senses more or less different from their original meanings. To the physiologist the phylogenetic origin of a tissue or the fundamental nature of a cell type is of no direct importance. Physiological anatomy is, therefore, of value to the physiologist rather than to the anatomist; Haberlandt's text, however, because of the thoroughness with which the ground is covered, is generally useful to all students who are able to "translate" the terminology.


Fig. 146.—Philippe Van Tieghem (1839–1914).

In the work of Eduard Strasburger (1844–1912), experimental physiology is combined with morphology in extensive cytological and anatomical studies. Though Strasburger is perhaps known best for his cytological contributions, his "Histologische Beiträge" contain the results of extensive and important anatomical researches. These relate chiefly to the conducting system of all plant groups, but especially of gymnosperms where his studies are very complete. In these papers he puts forward the idea of two distinct tissue systems, the cortical, or assimilating, and the conducting, or stelar.

The Stelar Theory.—The lack of a comprehensive presentation of the structure of the plant body as a whole, which is the outstanding weakness of De Bary's book, was supplied by the French botanist, Philippe Edouard Leon van Tieghem (1839–1914—Fig. 146) and his students, in the establishment of the stelar theory. Van Tieghem in 1870, before the appearance of De Bary's text, had already begun the presentation of a new way of looking at the general structure of the plant axis. In the following years he extended his observations, and elaborated his theory that both root and stem are fundamentally alike in structure, each possessing a distinctly limited central core, which he termed the stele, surrounded by a protective layer, the cortex. Van Tieghem's stele is limited externally by the pericycle, and his cortex includes the epidermis on the outside and the endodermis on the inside. The stele, both in roots and in stems, does not consist of vascular tissues alone, but also of "conjunctive tissue," in which the conducting tissues lie: in the roots, pericycle, pith, and the tissues between the primary strands; in the stem, pericycle, pith, and medullary rays. Van Tieghem pointed out that the stele was not so distinct in the stem as in the root, owing to the disturbance in the tissues caused by leaf traces, to frequent absence of the endodermis, and to variation in the pericycle.

Later, van Tieghem and his pupils elaborated the stelar theory, extending it to cover, in its modifications, all types of axes, and giving names to the varieties of stelar structure. They spoke of the type where xylem and phloem are arranged in a simple hollow cylinder as a *monostele*. Where such a stele is broken up radially by the invasion of the pericycle and endodermis, so that the cortex becomes continuous with the pith, and the segments of the cylinder are surrounded by the pericycle and endodermis, the stele, as such, is not obvious, except in outline; hence, an *astelic* condition is present. In astely, there is thus the appearance of a number of isolated steles in a parenchymatous matrix. Where such isolated strands become fused laterally, the endodermis and pericycle being lost between them, but united to form a complete ring on their inner side—as, for example, in certain species of *Equisetum*—a condition of fusion or *gamostely* exists. Where, in ontogeny, the monostele of the young plant forks, as the axis elongates, to form two or more strands similar to the first-formed stele, a *polystelic*, or *dialystelic*, condition is developed. Such polystely occurs in some angiosperms and in many ferns. Ultimately, the term "polystely" was, however, applied by van Tieghem to both the gamostelic and the dialystelic conditions. Strasburger supported van Tieghem in the chief features of the latter's stelar theory, but proposed the term *schizostely* to replace van Tieghems' astely.

With the establishment of the stelar theory a big step was thus made in a comparatively brief period toward the understanding of the fundamental grosser structure of the axis. That this step was fundamentally sound has been shown by the subsequent study of many students.

Van Tieghem, in his attempt to explain the variations of steles, adopted the basis of comparative morphology and phylogeny, the only basis on which a satisfactory explanation could be made. Chiefly in respect to the unity of all stelar forms as modifications of a single type, and as to the relations of leaf traces to the formation of broken steles, did van Tieghem fall short of a complete understanding of the theory. These conceptions, which are of the greatest importance to the stelar theory, were supplied in 1897 by Edward Charles Jeffrey, now professor at Harvard University. Professor Jeffrey, from an extensive study of all groups of vascular plants, and especially of the development of the stele in young plants, drew generalized conclusions concerning the nature of steles. Though agreeing in the main with van Tieghem concerning the nature of the stele he showed that the French anatomist's types had after all little morphological foundation. There are, he said, but two types of central cylinder, the siphonostele and the protostele; and these are fundamentally the same, since the former has clearly been derived from the latter. The protostele is a solid rod of vascular tissue in which a core of xylem is surrounded by phloem, and this by a pericycle; the siphonostele is similar to the protostele but is tubular, possessing a central pith, which Jeffrey claims arose phylogenetically as an invasion of the stele by the cortex. Thus the siphonostele is merely a modified protostele. Van Tieghem's types are but modifications of the siphonostele, the polystele not representing a "bifurcated epicotyledonary stele," nor the astelic condition the splitting of a monostele into definite bundles. The presence of breaks in the continuity of the vascular cylinder, which are related to the exit of leaf and branch traces and hence known as foliar and ramular gaps, is responsible for the apparent formation of distinct types of stele. Where the gaps are small, they may readily be overlooked, but where large, and when they overlap in longitudinal extent, the cylinder apparently consists only of isolated bundles. It is, however, a tubular network, perforated by extensive gaps. In the ferns, gymnosperms, and angiosperms, both leaf and branch gaps are always present, a condition Jeffrey termed "phyllosiphonic;" in the horsetails, clubmosses, and related plants, only branch gaps occur, the cladosiphonic condition.

Jeffrey claims that the pith is extrastelar in morphlogical nature, representing cortical tissue which has invaded the stele in its phylogenetic specialization. With the invasion of the stele by cortex, the phloem, pericycle, and endodermis also entered the core of xylem. Thus the primitive type of siphonostele possesses internal phloem, pericycle, and endodermis. With greater specialization, these become degenerate and may disappear, there remaining only a perimedullary zone to represent these tissues morphologically. The importance of Jeffrey's conclusions was immediately recognized; a satisfactory understanding of varied stelar structure could now be had, and the great value of this to all anatomy was evident. It explained, for example, for comparative and physiological anatomy the presence of vestigial internal phloem and endodermis; it brought out characters of the greatest importance in the phylogenetic relations of the large groups of vascular plants. Through the presence or absence of leaf gaps, together with other characters, Jeffrey made a new arrangement of the larger groups of vascular plants. The two groups thus formed, the Pteropsida and Lycopsida, have largely been accepted as natural, and their establishment has done much to aid in the determination of the phylogenetic relationships of the larger groups of vascular plants.

As to the method by which the pith arose in the protostele, a controversy arose between Jeffrey and certain English anatomists. Jeffrey's opponents claim that, at least in some groups, especially the eusporangiate ferns, the pith is not extrastelar, that is, cortical, in nature, but represents unspecialized xylem; that is, the pith is strictly stelar. The development of a pith in this way has been said to be by expansion, an unfortunate term, since it implies enlargement of the stele, a feature which does not necessarily exist. The discussion of the expansion and the invasion theories still continues sporadically, though it seems to be universally granted that in most plants the pith is doubtless cortical in nature. The establishment of the stelar theory has supplied a basis for an understanding of the structure of the plant body such as was not possible before. This alone has brought the vascular skeleton to the front as of much importance in the study of phylogeny.

Anatomy in Taxonomy.—The attention of anatomists was first called to features of internal structure as of importance in classification in the days of von Mohl; after the establishment of the theory of descent, the value of internal morphology in classification became increasingly evident. De Bary became one of the most prominent exponents of the anatomical method in taxonomy. The movement in this direction spread most rapidly in Germany as concerned living plants, and in England for fossil forms. The influence of the tendency to add anatomical features to the commonly used external morphological structure in taxonomy is evident in such important works as Engler and Prantl's "Die natürlichen Pflanzenfamilien" and Solereder's "Comparative Anatomy of the Dicotyledons."

Present-day Anatomy.—At the end of the nineteenth and the beginning of the twentieth century anatomical research turned definitely to the aid of taxonomists and morphologists in the solution of problems of natural relationship. Paleobotany, as a strong ally in this phylogenetic research, continued to stimulate progress in knowledge of anatomy through its constantly increased demand upon anatomy as a tool in the unraveling of the identity of fossil plants and of their relation to living forms.

During the past thirty-five years many prominent anatomists in England, France, and America have given their attention in greater or less part to problems of paleobotany. Perhaps the larger number of anatomists in these countries have, however, been more closely associated with the anatomical aspects of comparative morphology. The many studies of the vascular anatomy of the pteridophytes made in the first years of the century and carried on largely in relation to stelar theories, and to questions of the validity of classification in this group, were doubtless to a large extent responsible for the increased recognition of the importance of the vascular skeleton as indicating natural relationships. The determination of this importance may be said to be without doubt the great contribution of anatomy to the solution of the problems of phylogeny.

Because of this recognition of the value of the study of the vascular skeleton, anatomical research in America has centered about the stele and its vascular appendages, especially about the phylogenetic value of these important structures in their various modifications. In England also the viewpoint of phylogeny dominates the studies of prominent anatomists; in France, comparative morphology perhaps stands much as it has throughout recent years in that country, largely above other aspects of anatomy; in Germany, physiological anatomy, under the influence of Professor Haberlandt, chiefly holds sway in the antomical field.

To evaluate satisfactorily the anatomical research of the present time is clearly impossible. Moreover, even an outline of the contributions of the numerous individual investigators of today and of recent years is out of place in a brief and introductory sketch of this type. Therefore no attempt is here made to describe in detail the present situation in anatomy. Though the workers are many, the field is a very large one, the anatomy of the angiosperms being still largely unknown, and the opportunities for important contributions, both to descriptive and to comparative anatomy, are many.

Although at the present time the more "popular" fields of botanical research—physiology, cytology, and genetics—far surpass anatomy in commanding the interest of students, these fields are constantly demanding more and more complete information concerning structure. The requirements of these fields, together with those of applied botany, such as pathology and horticulture, must be met by anatomists; and all these fields must doubtless rely in the future in increased measure upon the information secured by morphology and anatomy.

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