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The development of botany in Germany during the nineteenth century.

EDUARD STRASBURGER.

AUTHORIZED TRANSLATION BY GEORGE J. PEIRCE.

[The following paper was published in 1893 in the second volume of the great and expensive work, *Die Deutschen Universitäten*, which the German Imperial Government prepared for the World's Columbian Exposition at Chicago. Its translation and publication in the BOTANICAL GAZETTE have been authorized by Professor Strasburger and by the Editor of the government publication in which it appeared. Since it forms the only supplement, so far as I know, to Sachs's "History of Botany," and brings the account to date, I have thought it would be extremely useful to American and English readers. The original publication is costly and not generally accessible, another reason for presenting it in English.—G. J. P.]

During the last half century Germany has been accorded a very high rank in botanical science. One evidence of this is that the botanical establishments of the German universities are able to congratulate themselves on being the resort of foreign botanists. It may safely be asserted that the impulses which, during this century, have carried botanical investigation into new lines, have been given in many cases by the teachers at the German institutions of learning. In purely systematic work England has held first place until recently, and now Germany is becoming her more and more successful competitor. The objects of botanical inquiry, like those in other departments of biology, were greatly affected by the theory of selection emanating from England, which Germany quickly accepted. For the theory of descent, which found fresh support in Darwin's theory of selection, the ground was well prepared, so far as botany was concerned, by Hofmeister's researches in comparative morphology.

The first decades of this century were devoted mainly to anatomical investigations, but at that time attention was

given almost entirely to the fully developed tissues and the solid cellular framework of plants. In the course of these researches the methods of investigation were improved, and observations were no longer made on crushed or torn objects, but on delicate sections. The improvements in microscopes, which were made at the same time, greatly aided such studies; and when one compares the figures made in successive decades, one sees how great have been the advances in the graphic reproduction of the objects seen. One may say that this sort of investigation of the plant body reached its fullest development during the thirties, and that the works of HUGO VON MOHL (of Tübingen, died in 1872) are its crowning achievements. By M. J. SCHLEIDEN (1839–1863 in Jena, died in 1881) the life history of plants was brought into prominence and declared to be the necessary foundation of every morphological conception. Schleiden's works were also the first in which the attention of investigators was directed to the cell-contents. From this time on, morphological study with the microscope began to develop in different directions; one which, at the same time that notice was taken of the development, was but the continuation of the former phytotomic researches, anatomy strictly so-called; another, which concerned itself with the cell-contents, cell-structure, and the origin of the tissues, histology; the third, whose main problem was the development of the members of the plant body, the solution of which was sought by the study of growing points and of forming embryos. These three directions were indicated by Schleiden and NÆGELI (of Freiburg and Munich, died in 1891), in part by the latter only. A contemporary of Schleiden, Nägeli excelled him in keenness of understanding, in critical power, and in observing faculty.

Nägeli's researches into the growth of the stems and roots of vascular plants, published in the year 1858, laid the foundations of plant-anatomy. In this work Nägeli developed from the purely morphological standpoint a classification of tissues, distinguished various types of growth, and finally traced the course and arrangement of the fibro-vascular bundles in the plant. Phytotomic investigation with morphology as the foundation was carried on by H. von Mohl, Schacht, Dippel, Frank, Count Solms-Laubach, Sanio, and von Hanstein. Of these, SANIO (a teacher in Lyck, in East Prussia, died in 1891) undoubtedly won most credit. His work, without the

least loss in value, was put somewhat into the background in 1877, when the "Vergleichende Anatomie" of A. DE BARY (at Freiburg, Halle, Strassburg, died in 1888), appeared. This book codified and extended our knowledge of plant anatomy, and established a nomenclature of the tissues which still holds good. The anatomical work of L. KNY (of Berlin), E. STRASBURGER (of Jena, now in Bonn), and H. SCHENCK (docent in Bonn) followed essentially the same direction.

Many celebrated investigators in other lands took part in the development of morphological phytotomy, but it is not for me to describe their labors here, since this can be a historical survey of the work of the German universities only, especially those of the German Empire. This limitation will naturally cause the sketch here presented to be very incomplete, and may even make it appear as though credit were given to the investigators at German institutions of learning for work in which they were merely participants with others. This possible reproach must be met by the frank acknowledgment of the limitations here necessary.

In contradistinction to that form of anatomy in which comparative morphological and, of late, in conseqence especially of Strasburger's work, phylogenetic characters were considered the essentials in estimating the importance of the tissues, there developed in the seventies the so-called physiological-anatomy. This new direction was given to the subject by SCHWENDENER (of Tübingen, now of Berlin) in his book "Das mechanische Princip im anatomischen Bau der Monocotylen," which was published in 1874. Schwendener's pupils work along this line, and the most talented of these, G. HABERLANDT (of Graz), attempted in 1884 to give a complete outline of physiological plant-anatomy.[1] Physiological plant-anatomy is a part of physiology, and as such it has led to conspicuous achievements. It has brought confusion into anatomy only in so far as it has attempted to establish its conceptions in the place of strictly morphological ones.

THEODOR HARTIG (Berlin, Brunswick, died in 1880), whose peculiar terminology rendered an understanding of his conceptions so difficult that they were often less regarded than they deserved, went his own way in the study of anatomy, though following essentially the morphological direction. Indeed, Th. Hartig was a keen observer, and many a discovery since made can be pointed out in his writings as a fact already known to him.

[1] Physiologische Pflanzenanatomie. Leipzig, 1884.—G. I. P.

The cell-theory which Schleiden set forth in 1838, soon showed itself to be defective, but it is nevertheless of great historical importance. It stimulated Th. Schwann to the microscopical investigations of the similarity in the structure and growth of plants and animals, which he published one year later; and it directed the attention of all to the contents of the cells. Soon Nägeli published his, for that time, remarkable researches into the formation and division of cells. H. Mohl also turned his attention to this new direction, exhaustively studied the appearance which the nitrogenous portions of the cell-contents display during their constant changes of form, found that they present for the most part the phenomena of streaming, and gave to them the name of *protoplasm.* In the year 1850, FERDINAND COHN (of Breslau) emphasized the identity of the contractile substance of animal cells with the protoplasm of plants, and this induced the zootomist Max Schulze, of Bonn, in 1863, to extend the name of protoplasm to the living substance in the whole organic kingdom. The minute structure of vegetable protoplasm was described by N. PRINGSHEIM (Jena, Berlin [2]) in a way which is valuable to this day, and our insight into its nature was thereby greatly advanced. On the other hand no investigations into cell-formation and cell-division, as they were conducted by Nägeli, Mohl, Pringsheim, Hofmeister, and others, could go beyond a certain point, and necessarily led in part to fallacious conclusions, so long as they were conducted on living, or at least not "fixed" objects. E. Strasburger was the first to conduct such investigations on suitably hardened material. In the first edition of his "Zellbildung und Zelltheilung" in 1875, this method was systematically employed. Combined with the most extended investigations, which included the whole vegetable kingdom, and parts of the animal kingdom as well, this method led to general results which applied to the whole organic realm. This publication stimulated manifold researches, especially by the animal histologists, which extended, and in various ways corrected, the statements of its author, without, however, impairing the value of the most important results therein set forth. Strasburger himself, in the third edition of the book in 1880, was able to trace back free cell-formation to the general phenomena of the origin of cells; and in subsequent

[2] Died in Berlin, October 6, 1894.—G. J. P.

publications, he pursued the further development of the question. While the material studied for the first publication of the book was nearly all unstained, in further observations stained objects were used, and in the course of these investigations microscopic technique made not the least important of its advances.

From the moment when the attention of investigators was turned to the contents of cells, further researches into the nature of the bodies enclosed within the body of the cell itself had to be undertaken. Special studies of starch-granules, chlorophyll bodies, aleuron-grains, and the like, were made by Nägeli, J. Sachs, Th. Hartig, W. Pfeffer, W. Schimper, Fr. Schmitz, Arthur Meyer, Zimmermann, and others. In this series the discovery of the amylogenic bodies by W. SCHIMPER (of Bonn), was of fundamental importance.

Nägeli's mathematical talent, and his desire to fathom the causes of these phenomena, led him to deduce from the phenomena of swelling, double-refraction, growth, and from the visible structure of stratifications and striations, a theory as to invisible structure of organized bodies. The stratification of cell-membranes has since been shown by DIPPEL (Professor at the Polytechnic School in Darmstadt), FR. SCHMITZ [3] (in Greifswald), Strasburger, NOLL (docent in Bonn), and KRABBE (docent in Berlin), to be due to growth by apposition. Although the theory of growth by intussusception is no longer held in the sense in which Nägeli conceived it (for the double refraction of organized bodies has presumably other causes than those assigned by Nägeli), yet his micellar theory remains as a brilliant conception which must hold a high place in the history of our science. Recently Wiesner (of Vienna) has put forth other views as to the elementary structure and the growth of living-substance, which are quite opposed to those of Nägeli. On the other hand, G. BERTHOLD (Göttingen) has sought by his studies in the mechanics of protoplasm [4] to explain by physical causes the structure, the formation, and the movements of the body of the living cell. Similar investigations of the zoological aspects of the question have been published by Bütschli and by the physicist Quincke. The chemical constituents of the living cell have occupied the attention of REINKE (Göttingen, now in Kiel), ZACHARIAS (of

[3] Died January 28, 1895.—G. J. P.

[4] Studien über Protoplasmamechanik; Leipzig, 1886.—G. J. P.

Strassburg), and especially of FRANK SCHWARZ (at the Forestry Academy at Eberswalde).

The tendency to give a mathematical aspect to observed phenomena controlled Nägeli's investigations of apical growth, which he published in 1845. In a similar way, but with independent broadening and deepening of the problem, W. HOFMEISTER (Heidelberg, Tübingen, died in 1877), followed the course of development of the organs of the plant from the processes of division which take place in growing points and embryo and in 1851 published his now famous comparative researches on the germination, development, and fruiting of the higher cryptogams, and the formation of seeds in the Coniferæ. Those researches laid the foundations for a phylogeny of the vegetable kingdom ten years before the appearance of Charles Darwin's "Origin of Species." The value of a knowledge of development, of morphological comparisons based on exhaustive investigation, was thus set in a new light, and a broad field was opened for further study. That many single statements in this book were erroneous does not in any way diminish its value, for this rests on the broad foundation of the whole work.

Hofmeister's remarkable ability to comprehend the homologies of the most remote divisions of the vegetable kingdom, gave permanent value to his morphological comparisons. At the same time, the gulf which seemed to separate the cryptogams from the phanerogams was bridged by Hofmeister's discoveries, and the processes which take place in the formation of the embryo among phanerogams, were set in their proper relations with the alternation of generations among the higher cryptogams. In the field thus opened by Hofmeister, Pringsheim labored with similar objects in view, but with limitations of the problem, and his achievements are now classical in every detail. Gaps in our knowledge have been closed by the valuable contributions of METTENIUS (Leipzig, died in 1866), CRAMER (of Zürick), von Hanstein, Kny, and Strasburger. LEITGEB (of Graz, died in 1888) devoted to the Hepaticæ seven full years of the most careful study along similar lines. The value of these researches, which laid bare the origin, development and homologies of the organs of the plant, will be permanent, despite the fact that the early investigations, inaugurated by Nägeli, of the processes of division

which take place at the vegetative point have lost the importance which was once attributed to them; for Sachs has shown that the arrangement of the elements at vegetative points is not of morphological significance, but is controlled by mechanical conditions.

Schleiden's investigations into the formation of the embryo of phanerogams, which date from the year 1837 on, led him curiously astray. He considered that the embryo originated from the tip of the pollen-tube, and that the ovule was merely the place in which it was further to develop. If this were so, then there would be no sexuality in plants, and a comparison with the phenomena of fertilization in the animal kingdom would be quite out of the question. Schleiden's views found warm defenders, but in 1849 Hofmeister came out clearly in opposition to him, in a very comprehensive work. (Amici, in Italy, had already in 1842, taken such a stand). Hofmeister proved beyond controversy that the egg (germinal-vesicle) was already formed in the ovule, and that it was fertilized by the contents of the pollen-tube. He did not arrive at the current notion of the structure and phenomena of the sexual apparatus. These were first made clear by Strasburger in 1877. In the same paper Strasburger showed also that the hitherto supposed cases of parthenogenesis among phanerogams were due to the adventitious formation of embryos by non-sexual branching of the nucellar tissue into the cavity of the embryo-sac. Since the number of such branchings is indefinite, it is at once evident why, in the supposed cases of parthenogenesis, polyembryony is so common. Two years before (1869) it had already been demonstrated by Strasburger that the so-called corpuscula of the Coniferæ are true archegonia, and that their contents represent a single egg.

In 1880 KARL FRIEDRICH SCHIMPER (a scientific man who occupied no public office, and who died in 1867, at Schwetzingen) established the new theory of phyllotaxy, which attracted due notice, and became further developed and carried to formal completion in the writings of ALEXANDER BRAUN (Freiburg, Berlin, died in 1877). This theory assumed, in consequence of Braun's idealistic conception of nature, the form of abstract principles which controlled the processes of development in the body of the plant. Hofmeister was the first, in 1868, to attempt to explain the observed regularity in the

arrangement of members on a common axis, and their spiral sequence, by reference to definite mechanical causes. The mechanical basis for the theory of phyllotaxy was completed in Schwendener's writings (1878), which showed that mechanical and geometrical conditions, especially the pressure exerted upon one another by the young members forming on the common axis, control the regularity of their positions in relation to each other. In the same way K. SCHUMANN (Custodian in the Botanical Museum at Berlin) is now attempting to explain the arrangement of floral organs.

Closely akin to Braun's work, in that he established certain types, which, however, he considered to be phylogenetically the true starting points of later variations, W. EICHLER (Graz, Kiel, Berlin, died 1887) published in 1875 and 1878 the two volumes of his "Blüthendiagramme." These are founded on general comparative investigations of the mature form, supplemented by a study of the development. From a similar stand-point PAX (Custodian in the Botanical Garden at Berlin), wrote his "Handbuch der allgemeinen Morphologie der Pflanzen" which appeared in 1890. K. GOEBEL (Rostock, Marburg, Munich), on the other hand, tried in his "Entwickelungsgeschichte der Pflanzenorgane," published in 1883, to be independent of the morphological ground-plans, to consider the distinct members of the body of the plant for themselves, and to be directed in their comparison only by the homologies. Development and comparative morphology are to him the most important aids in organography.

Although the philosophical element in Braun's most important work, concerning rejuvenation in nature, published in 1851, is contrary to the principle of cause, which is now the basis of scientific thought, yet this work still holds attention because of the freshness of its descriptions and the affectionate absorption of the author in his problem. For this reason the work contributed no slight stimulus to the further study of the lower cryptogams, especially of the Algæ. Thuret performed certain experiments in 1853 which demonstrated the sexuality of the *Fucaceæ*, but he attributed fertilization to the effects of the contact between spermatozoid and egg. Pringsheim was the first to show, in his researches published in 1855, that in generation "a mingling of the whole spermatozoid mass with the fructifying sphere takes place." Important works by Pringsheim, which made clear the whole

development of various groups of algæ, and of the alga-like *Saprolegniæ* followed in subsequent years. Other valuable researches by Ferdinand Cohn, de Bary, PFITZER (Heidelberg), Goebel, Berthold, Fr. Schmitz, Reinke, and other German investigators supplemented them, but in 1869 Pringsheim made another remarkable contribution to this field of knowledge by his discovery of the copulation of gametes (zoospores).

Early in the sixties the impulse to a reform in the study of the Fungi was given by de Bary in Germany, while Tulasne had already done the same in France. It was de Bary who, more than any one else, perfected the methods of investigating the Fungi, directed researches into decisive lines, and laid the foundations for the results which this department of knowledge was soon able to show. After him O. BREFELD (Münster) took the lead by his achievements in this field, and since 1872 has devoted himself to studying the development of fungi, beginning with a single spore and tracing its development to the end. Brefeld's methods, extended and adapted to the field of bacteriology, have produced great results. De Bary first effected the artificial infection of a host by a fungous parasite, but Brefeld was the first to succeed in cultivating typical parasites in nutrient solutions, thus making them saprophytic. By de Bary's investigations, our notions of the alternation of generations among the Fungi were brought within the true limits, while Brefeld leveled the ground for the construction of a natural classification of the Fungi, and considerably limited the statements as to sexual differentiation in this group.

The demonstration of the fact that lichens are symbiotic double organisms, depending upon the union of ascomycetous (rarely hymenomycetous) fungi with algæ, attracted general attention. In 1860 and 1868, in the first two parts of his researches into the lichen thallus, Schwendener declared the gonidia to be the terminal cells of short lateral branches of the hyphæ. In 1866 de Bary led up to the true idea of the lichen thallus in the gelatinous lichens, and spoke the words which solved the whole problem and brought about the right conception of all lichens. This final step was taken by Schwendener in the supplement to the last part of his "Flechtenstudien," and was repeated still more decisively in his "Algentypen der Flechtengonidien," published in 1869. In basing this conception on studies in development, STAHL (of Jena) has

won most credit in Germany. Further questions as to the presence of sexes in lichens, and as to the structure and development of their organs of fructification, have been pursued especially by Stahl, FÜNFSTÜCK (docent in Stuttgart), and G. Krabbe. Alfred Möller succeeded in Brefeld's laboratory in cultivating lichens saprophytically, and without the algæ, in nutrient solutions.

The appearance in 1865 of "Die Experimentalphysiologie der Pflanzen," by JULIUS SACHS (Freiburg in Baden, Würzburg), marked an epoch in the development of vegetable physiology. The work at once restored vegetable physiology to its place at the center of scientific research, whence it had been pushed aside by the increased interest in anatomical investigation. The work did this the more successfully since it contained not merely a clear and well arranged review of the achievements of former times, but also the fundamental investigations of its author which extended to nearly all of the divisions of physiology. The number of physiological researches which were then carried on by Sachs himself, and by his pupils, grew from year to year, and were for the most part published in the Arbeiten des botanischen Instituts zu Würzburg. These researches concerned all divisions of physiology, but especially the relations of plants to those external forces which operated upon them. PFEFFER (Basel, Tübingen, Leipzig) developed especially the physical side, and during the last twenty years has produced a series of most remarkable works. His investigations of the chemotactic movements awakened special interest, for they explained, at a single stroke, as the attraction of definite organisms by chemical substances, the until then enigmatical influence which the sexual products exert, even at a distance, upon each other. His "Handbuch der Pflanzenphysiologie," which appeared in two volumes in 1881, at once became indispensable to every botanist. GEORG KLEBS (of Basel) has since then especially developed the physiology of the vegetable cell; phototactic phenomena were exhaustively studied by Strasburger and Stahl; W. DETMER (of Jena), and W. Schimper have distinguished themselves in the field of physiology of nutrition, and many valuable contributions to our knowledge of this subject have been made by B. FRANK (professor at the Agricultural College in Berlin). We are indebted to A. HANSEN (of Giessen) for good chemico-physiological contributions,

Besides Sachs, ROBERT HARTIG (of Munich), Schwendener and Strasburger have especially interested themselves in the problems of the movement of water in the plant; while ALFRED FISCHER (Leipzig), and others have been concerned with the transfer of food-materials. Concerning the physiological phenomena of irritability, in addition to the fundamental labors of Sachs, the researches of WORTMANN (professor at the Academy in Geisenheim), of VOCHTING (Basel, Tübingen), and especially of FR. NOLL (docent in Bonn), have found well merited respect.[5] An attractive presentation of our entire physiological knowledge was given in Sachs's "Vorlesungen über Pflanzenphysiologie,"[6] the first edition of which was published in 1882. The phenomena of the irritability of the living substance were there thoughtfully set forth, and their importance in the true estimation of the phenomena of life clearly elucidated.

Our knowledge of the reproductive processes has gained merely a firm morphological basis. Strasburger especially has contributed to this during recent decades. The physiology of reproduction is still, for the most part, on speculative ground; but it was notably advanced in 1884 by Naegeli's mechanico-physiological theory of descent, in which the idioplasm theory was first formulated. Naegeli's observations on the production of bastards, on the conditions for the appearance of species and varieties, and his studies, extended through years, of the intermediate forms among the Hieraciums, are to this day important contributions to the phenomena of genera and development.

Thanks to Darwin's classical work on the arrangements for pollination among the orchids, the attention of students was directed to a very remarkable book by Christian Konrad Sprengel which, published in 1793, remained quite unnoticed and had practically disappeared. In all parts of Germany, workers turned their active attention to this subject, and in consequence, Sprengel's assertions were generally confirmed, often extended, and in many essential points given their correct significance. FR. HILDEBRAND (Freiburg in Baden) was the first to distinguish himself in this direction; but HERMANN MÜLLER (teacher in Lippstadt, died in 1883)

[5] No one will doubt that Pfeffer's name was only unintentionally omitted, and that it deserves a prominent place in this list.—G. J. P.

[6] Translated and published in English in 1887.—G. J. P.

especially did so in the numerous writings in which he described the arrangements for pollination in flowers. This is still a promising field for investigation, and busies many students, merely to name whom space here forbids.

The investigation of the phenomena of pollination of flowers, and of the striking adaptations between flowers and insects, which here present themselves to students, greatly promoted the study of adaptations in general. These are now comprehended under the general name of biology but, under the name of ecology or the study of adaptations, would better form a part of physiology. We are indebted to Hildebrand, Stahl, VOLKENS (docent in Berlin), but especially to Goebel and Schimper, for valuable contributions to this subject. The last named has contributed material of remarkable value bearing upon the problems of plant-geography. A distinct field of physiology was opened by Vöchting's striking work on the apex and base of plant members, on the inner polarity of the plant body, and on the related phenomena of regeneration.

[*To be concluded.*]

Bonn, Germany.

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