flowers that were too young having been examined, have been un-
fortunately described by Hasskarl as two-celled with parallel cells; it
is doubtless this unhappy misapprehension that has led both De
Candolle and Miquel to look upon *Anthocoma* as a *Gomphostemma*,
and that has obscured so completely and so long the true affinities of
Zollinger's plant.

DAVID PRAIN, Calcutta.

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**NOTICE OF BOOK.**

E. STRASBURGER: UEBER DEN BAU UND DIE VER-
RICHTUNGEN DER LEITUNGSBAHNEN IN DEN
PFLANZEN. Histologische Beiträge, III; Jena, Fischer,
1891.

Professor Strasburger, who for many years devoted himself almost
exclusively to the investigation of the problems of minute histology,
has in the present work made the most important recent contribution
to the anatomy and physiology of vascular plants. If some of his
former researches may claim a wider interest, as dealing with questions
which are common to both the organic kingdoms, his latest book is,
from a purely botanical point of view, of at least equal importance.
This is owing, not only to the value of the special results attained, but
also to the fact that this book presents the most striking example
in botanical literature of combined anatomical and physiological
investigation.

As a rule the anatomist and the physiologist work independently.
The former either tends to ignore function altogether, or perhaps is
too ready to infer function from structural evidence alone, without the
test of experiment. The physiologist on the other hand has often
trusted too exclusively to experimental methods, and has perhaps
even treated anatomical details with a certain contempt. There are
few men who are capable of equal success in both directions; among
these few Prof. Strasburger is the most distinguished.

The motive of the book, and the point of view of the author, are
made clear in the preface. Some years ago Prof. Strasburger began
experiments on the vexed question of the ascent of water in the wood. He became absorbed in the problem, and in order to obtain a firm basis for the investigation, found it necessary to undertake a minute anatomical examination of the conducting tissues. This part of the enquiry occupied fully two years (a short enough time considering the magnitude of the results attained), and involved the consideration of purely morphological questions. Subsequently, in the light of these anatomical data, the physiological experiments were taken up again, and led to conclusions of the greatest importance.

The author has made a point of strictly severing the morphological from the physiological side of his problem. He points out that the morphology of the tissues, like that of external organs, must be entirely uninfluenced by considerations of function. The task of morphology is to trace the derivation of one form from another, to refer different forms to a common origin. This is essentially a question of phylogeny; it can only be dealt with by means of the comparative method, and by the study of individual development. To these the reviewer would be disposed to add the direct evidence of palaeontology, which on the anatomical side is by no means unimportant.

The one object then of morphological anatomy is to establish the homologies of the tissues. There is also a physiological anatomy which has the equally important task of classifying the tissues by their functions. It is necessary to keep the two objects distinct, and to realise that a physiological classification has nothing to do with morphology.

Prof. Strasburger's clear exposition of the twofold purpose of anatomy is likely to be very serviceable. The mere description of internal structure, is in itself just as barren as that of external form, and anatomy in this narrow sense, has no claim to the rank of a science, as Nägeli long ago pointed out. The value of anatomy depends on the facts that it is at once an integral part of morphology, and the necessary basis of physiology.

The book contains about 1000 pages, which are almost equally divided between the anatomical and physiological portions. The first part begins with an extremely full investigation of the structure of the vegetative organs in Coniferae. It is only possible to enumerate a few of the most striking results here, though the completeness of the description is perhaps its greatest merit.
It is already known that many of the Abietineae have medullary rays of complex structure, the wood-rays containing water-conducting tracheides, as well as living parenchymatous cells. On the other hand we also know that most Coniferae have bordered pits on the tangential surfaces of the latest formed autumn-wood. The author shows that the development of these two structures varies inversely. All Conifers which are destitute of tracheides in their rays, form tangential pits on their autumn-wood, while those in which the ray-tracheides are best developed, have few or no tangential pits. Both structures in fact serve the same purpose of providing a radial connection between the water-conducting tissues of successive annual rings.

The author confirms Russow’s observation of the constant presence of intercellular spaces, containing air, between the elements of the rays, both in Gymnosperms and Dicotyledons. The living cells of the rays communicate by pits with these spaces, which are continuous through the cortical tissues with the lenticels or equivalent openings in the periderm. Thus the respiration of the deep-seated living elements of the wood is provided for.

Among the most important of the author’s discoveries is that of the physiological representatives of the companion-cells, in Gymnosperms, in which these elements, as such, are never present. The chief conclusions (some of which the author published in a previous paper) are here summed up as follows: (p. 55)

In the Abietineae the functions of the companion-cells are fulfilled by certain rows of cells belonging to the medullary rays of the phloëm. In a portion of the Cupressineae and Taxodineae these functions are divided between the specialized ray-cells and other series of elements forming part of the bast-parenchyma. In the remainder of these two tribes, and in the whole of the Taxineae and Araucarineae it is the bast-parenchyma alone which is concerned. In all these cases the function of the cells in question is inferred from their especially abundant protoplasmic contents, from the entire absence of starch when they are fully developed, from the fact that they reach maturity simultaneously with the sieve-tubes, and also become emptied and obliterated at the same time with them; lastly, from the fact that they are connected with the sieve-tubes by pits of peculiar structure, resembling one-sided sieve-plates. As regards the sieve-plates themselves, the author decides that in the Coniferae they are never really open in the functional sieve-tube. The plug of swollen middle-lamella
by which the continuity of the protoplasm is interrupted, does not, he believes, offer any hindrance to the passage of dissolved substances, though it renders the transference of living protoplasm impossible.

The callus is stated to be formed directly from the protoplasm; it is regarded as a by-product, rather than a reserve-substance; in some cases it becomes of functional importance as effecting the temporary closure of the sieve-pit.

The arrangement, both of the true companion-cells in Angiosperms, and of their representatives in Gymnosperms, shows that they cannot serve for the longitudinal conduction of food-substances. Their function is rather to receive the albuminous material conveyed by the sieve-tubes, and ultimately to pass it on to developing tissues.

The author finds that the arrangement of the sclerenchymatous elements in the bast of most Conifers is such as to exclude the possibility of mechanical function. In such cases these elements are regarded as serving simply for the deposition of excessive cellulose, formed as a necessary result of metabolic processes in the starch-containing cells (p. 77). It is difficult to believe in so great a waste of carbohydrate material, and some local mechanical use (e.g. the hardening of the bark) may perhaps be conjectured.

Prof. Strasburger points out that the primary structure of the phloëm in Abietinae resembles the permanent structure in Araucarineae and Taxineae. This anatomical fact, in connection with other morphological points, and with the results of Palaeontology, leads the author to regard the two latter families as relatively primitive forms, and the Abietinae as the most modified group of Conifers.

The careful re-investigation of the leaves of Coniferae has led to some interesting results, of which the most important is perhaps the discovery of 'albuminous cells' forming an extension of the phloëm of the leaf-bundles, just as the transfusion-tracheides form an extension of their xylem. These albuminous cells no doubt have the same function as the terminal phloëm-elements of the fine branches of the bundle-system in Angiospermous leaves. In both cases this function is to absorb from the mesophyll the nitrogenous products of assimilation, which are destined to be conducted elsewhere by the sieve-tubes.

In Pinus the central-cylinder of the leaf is alone continuous with the stem. Hence all the assimilated food must pass through the tissues of the cylinder (vascular bundles and conjunctive parenchyma). This observation leads to a general discussion of the internal morphology
of stem and leaf, which is of fundamental importance. All the parts of the central cylinder of the leaf in *Pinus* are continuous with the corresponding tissues of the stem, and ultimately with those of the root. It follows (p. 111) that in *Pinus* two tissue-systems, that of the central-cylinder and that of the primary cortex, run separately throughout the entire plant. This morphological separation coincides on the whole with distinctness of function. The cortical tissue is the great assimilating system; the central-cylinder assumes the function of conduction. ‘As it is in *Pinus*, so is it in essentials in all vascular plants, while the distribution of the two tissue-systems in the plants, and their mutual delimitation, are also facts of general application.’

Thus the point of view of the French anatomist Van Tieghem is definitely adopted by the chief German authority; the central-cylinder is recognised as an anatomical region of the first order, of which the vascular bundles are subordinate parts. The importance of this conception, which profoundly modifies the anatomical teaching of Sachs and De Bary, is evident all through the book.

A section on the vegetative structure of Gnetaceae brings out the general agreement with Dicotyledons rather than with Gymnosperms. The chief anatomical characters which indicate the true gymnospermous affinities, are to be found in the structure of the phloëm, and in the indications of transfusion tissue in the leaves.

The investigation of the Cycadeae has not yielded much which is new. The structure of the phloëm is that of the simpler Coniferae.

The anatomy of a large number of dicotyledonous types is described in the fullest detail. The value of these minute researches can scarcely be fully appreciated except by those who are themselves engaged in such investigations, a remark which applies in a great degree to the whole book. The wood of Dicotyledons turns out to be even more complicated than was supposed before. In many of these plants, for example (e.g. *Salix*), both the medullary rays and the xylem-parenchyma consist of two kinds of cells. In the case of the rays they may be distinguished as horizontal and vertical cells. The former contain abundant starch, and communicate by pits with the intercellular spaces, but not with the vessels; the latter are destitute of starch in summer, and are in communication with the vessels, but not with the intercellular spaces. The former serve chiefly for the conduction of assimilated substances, and for gaseous interchange; the latter communicate with the tracheal system. This communication serves
a double purpose; first, to supply the living elements themselves with water, and with certain salts, especially phosphates, which they can directly assimilate (p. 868); and further, to allow of the passage of organic substances, especially carbohydrates, into the tracheae, by which they are rapidly conducted to the growing regions, at least during the spring (p. 894).

The Vine is studied with special minuteness, and among many points of interest the author calls attention here to the emptying of the sieve-tubes and companion-cells in winter, a fact which is quite inconsistent with the function of food-reservoirs, attributed to these elements by Frank and Blass.

The description of the wood of the Oak brings out a point of the highest morphological importance. The author regards the xylem generally as consisting primarily of two forms of tissue only—the tracheae and the parenchyma. In the great majority of woods the mechanical elements (fibres) belong to the parenchymatous system, as is indicated by their simple pits, and proved by the presence of transitional forms. In the Oak, however, and probably in all Cupuliferæ, as well as in Rosaceae and a few other cases, the so-called fibres have bordered pits, and pass over through intermediate forms into the tracheides. In these cases, in fact, the mechanical elements are homologous with the tracheal system, while in most woods they have arisen by modification of the parenchyma. This shows well how misleading a physiological classification of tissues may be from a morphological point of view.

The author's conclusions as to the wood are also extended to the bast. Here we have on the one hand the cribral system, to which the sieve-tubes and their companion-cells (if present) belong, and on the other the parenchymatous system, from the modification of which the bast-fibres have been derived. In the Gymnosperms, however, we have seen that the functional equivalents of the companion-cells belong to the parenchymatous system. Similar views of the morphology of the phloëm had already been expressed by Lecomte.

The phloëm of Cucurbita has once more been fully investigated. Here also the author finds that the callus is derived directly from the protoplasm, its formation beginning in the pores of the sieve-plates. The function of the living protoplasmic layer lining the walls of the sieve-tubes consists, according to the author, in preventing diffusion
from the tube, and in providing material for the formation of callus in order to close the plates when necessary. From the fact that the upper phloëm of the bicolateral bundles in the leaf of Cucurbita is already empty at a time when the normal lower phloëm is in full activity, it is inferred that the former fulfils its function during the development of the leaf, serving to conduct to it the necessary food-supplies, while the normal phloëm is alone concerned in conveying the products of the leaf's own assimilation. It will be interesting to observe how far this distinction holds good in other cases of double phloëm.

In describing the anatomy of various Ranunculaceae the author calls attention to the close agreement in structure between the vascular bundles of this order, and those of the Monocotyledons.

The first monocotyledonous type described is the familiar Zea Mais. The course of the vascular bundles is traced in detail, and it is shown that each bundle thins out greatly before fusing with one below it. Hence at every point of fusion there is a marked constriction of the water-conducting channels. From this fact, as well as from many other observations and experiments pointing in the same direction, the author infers that very narrow tracheal strands are sufficient to conduct the ascending current of water. The large vessels are important for storage rather than for conduction.

The phloëm of the bundle, as well as its xylem, tapers in the downward direction. The effect of this is that each row of sieve-tubes and companion-cells is in its turn brought into contact with the surrounding parenchyma, to which it can thus pass on the nitrogenous food-supplies.

The anatomy of several Palms is investigated, and it is shown, in agreement with Eichler, that when growth in thickness takes place it is due entirely to the extension of the inter-fascicular parenchyma.

The Monocotyledons with true secondary thickening receive much attention. The author points out that the thickening-ring here differs from the true cambium of Dicotyledons or Gymnosperms in the fact that there is no single initial row of cells to the divisions of which all the secondary tissues can be traced. On the disputed question of the nature of the secondary 'tracheides' in these plants, Prof. Strasburger entirely confirms the opinion of Krabbe and Röseler, that these elements are really tracheides, formed by the elongation of single cells, and not 'short vessels,' arising by cell-fusion, as was maintained by Kny and others. Some valuable observations on the remarkable
secondary growth of the roots of these plants are recorded, some of which, however, were anticipated in the first edition of the author's "Practicum."

The anatomy of vascular Cryptogams is disposed of rather rapidly. As regards Equisetum a new interpretation of the structure of the bundle is given. It is also proved that here, as in Grasses, the intercellular space accompanying the xylem is always filled with water, not with air, even in those species in which each bundle is enclosed within an endodermis of its own.

Van Tieghem's interpretation of the prevailing structure of the stem in Ferns as 'polystelic' (each 'concentric bundle' of De Bary representing an entire cylinder like that of a root), is adopted by the author, who, however, differs from the French anatomist as to the morphology of the phloëm-sheath. This layer is regarded by Prof. Strasburger as constantly belonging to the cortex, while Van Tieghem finds that in many Ferns it is the homologue of the pericycle. That the phloëm-sheath and endodermis are often sister-layers is certain, but it is possible that in these cases both layers may belong to the cylinder, as was suggested by J. E. Weiss. These difficulties of delimitation occur in all morphological questions, and no doubt the problem is often insoluble.

In many Ferns the tracheides form a thick and uniform strand, in which no living cells are interposed, so that there at any rate there is no room for the vitalistic theory of water-conduction.

The central cylinder of Lycopodium is regarded as 'gamostelic,' in Van Tieghem's sense, i.e. as representing a fusion of a number of 'steles' like those of Selaginella. This view does not appear to rest on any sufficient developmental or comparative evidence, though as a mere description of the mature structure it is appropriate enough.

The author devotes a chapter to a summary of his anatomical results, but this has been to a great extent anticipated in our survey. We have already called attention to the adoption of the general anatomical conceptions of Van Tieghem. It is unnecessary here to follow the discussions which have arisen between the two investigators on points of detail. The idea of the cylinder or stele as a primary anatomical region, superior to the vascular bundles, appears to the reviewer to be a fruitful one, chiefly for two reasons. First, it enables us to understand the homologies between root and stem, which were to a great extent obscured by De Bary's treatment of the central-
cylinder of the root as a single ‘radial’ bundle. Secondly, it throws
great light on the structure of the lower vascular plants, in which we
may either have a single cylinder, not differentiated into individual
vascular bundles at all, as in the simpler Ferns and in the fossil Lepi-
dodendra, or a number of cylinders, each complete in itself. The
confusion of these latter (under the name of concentric bundles) with
the vascular bundles of the higher plants was another weak point in
the anatomy of De Bary’s school. On these main questions it seems
pretty certain that the anatomy of the future will follow the lines of
Van Tieghem and Strasburger; the differences between them are com-
paratively of trifling importance.

A chapter on the connection of the vascular bundles as affected by
the growth in length and thickness in the stem and root, does much,
with the help of the diagrams, to clear up this rather difficult subject.
It is pointed out that the protoxylem of each new shoot is continuous,
not with the protoxylem of the next older shoot, but with its later-
formed wood. In this way only can a continuous water-channel be
maintained, for the protoxylem of the older parts will have already
become disorganized and useless, at a time when a new shoot is
formed. Similar considerations apply to the phloëm. In the stem the
new layer of thickening from the cambium, starts each year from the
top, in immediate connection with the vascular bundles of the young
shoots, and thence advances down the tree. The reason why the
outer zones of secondary wood are always the most active in conduc-
tion, is because these alone are in direct continuity with the youngest
shoots and their leaves. So far as the wood is concerned this is
modified by the presence of tangential pits, and similar contrivances;
in the phloëm there is usually no such provision for communication
between successive zones; hence, as a rule, only the youngest layer
of phloëm, which is in direct connection with the leaves, is functional.
This does not of course apply to Monocotyledons without secondary
thickening, in which the same phloëm may remain active for years.

A section on the width and length of vessels introduces the strictly
physiological portion of the book. On the former point there was
not much to be done. The widest vessels, as De Bary had already
shown, are always pitted vessels with short joints. The greatest di-
mensions were found in a leguminous liane (Mucuna) where the
vessels attain 0.6 mm. in diameter.

The determination of the length of the vessels was a more difficult
matter. The method adopted was to inject pieces of the stem with mercury, under pressure, and to observe the length of stem through which the mercury could be made to pass, and the number of vessels through which it escaped, on the lower cut surface. The general result is that while the vessels vary much in length they are on the whole much shorter than De Bary and most anatomists supposed. Among the longest vessels are those of the Oak, which are often two metres in length, and some of which may even extend the whole length of the stem. This, however, is an extremely rare case; in almost all plants the length of each continuous vessel is a mere fraction of that of the entire path of conduction.

Of the physiological half of the work the greater part is devoted to the question of the ascent of water in the wood. A repetition of the familiar 'ringing' experiments was first undertaken, with the result of proving once more that only the wood conducts the water-current, and that in the wood only the living albumen is functional. In spite of this latter fact the author, on the ground of experiments to be mentioned below, does not admit that living cells take any part in the conducting process. The non-conductivity of dead wood depends on its comparative dryness, not on the absence of living elements.

Some general remarks on the whole question serve to define the author's point of view, and to introduce the experimental work. Prof. Strasburger, having convinced himself that the water-current passes through the cavities of the tracheae, was at first disposed to accept the 'vitalistic' theory, according to which the protoplasm of the living wood-cells, either by active contraction, or by its influence on osmosis, plays an essential part in pumping up the water. His experiments, however, have led him to the opposite conclusion, that the ascent of water in plants is a purely physical process, though one of which Physics is not at present able to give a full explanation.

The author has certainly established a very strong case, and in the face of his experiment the theories of Westermaier and Godlewski no longer appear tenable.

He summarises his results as follows (p. 539):—That the ascent of water in the plant is a physical and not a vital process was first proved by experiments with plants more than 10½ metres in height, which were caused to take up poisonous solutions. Corresponding results were attained with plants previously killed by other methods. The conditions necessary for the ascent of water are: (1) that the
cell-walls should be in a state of imbibition, (2) that the cavities of the tracheae should be to a certain extent filled with water, and (3) that they should be isolated, so as to exclude the entrance of air. Atmospheric pressure helps to keep the water suspended, but does not cause its ascent. Transpiration is only important in so far as it makes room for the ascending water. Should the supply of water be deficient, certain of the tracheal channels are emptied and closed. In such closed tracheae a very low pressure prevails, which is maintained until they can be refilled with water. The difference between the atmospheric pressure and that in the tracheae, great as it is, is not usually sufficient to force air into the emptied elements. Root-pressure is not immediately concerned in the ascent of water.

As the insufficiency of capillarity has long been established, we are led, as the net result of the most elaborate investigation of the question which has yet been made, to a purely negative result; the cause of the ascent of water in trees is still unknown. A great point is however gained, if we may take it as proved that the process is a purely physical one. The protoplasm, which is responsible for so much, has at least been relieved of one strictly mechanical function, and the problem of the sap is thus brought within a measurable distance of solution. The author's work does indeed afford some indications (e.g. the movement of the film of water between the air-bubbles and the walls of the tracheae) which, if taken up by physicists, may, he hopes, lead to the long-sought explanation.

The details of the experiments must be read in the original. A summary of them would far exceed the limits of this review. In every case the minute acquaintance which the author has gained with the anatomy of the plants investigated has proved to be of the greatest value, and gives a special character to his investigations.

The following passage, bearing on some of the most crucial experiments, may be quoted (p. 623):—‘The fact that trees up to 20 metres in height, can, without the assistance of root-pressure, take up for weeks together a substance so poisonous as a 5-10% solution of copper sulphate, and conduct it through their stems, which were of necessity killed within the first days of the experiment, shows clearly that the living elements of the wood can have nothing to do with the raising of water, and that this process is a purely physical one. On the other hand it may be assumed, on physical grounds, that atmospheric pressure and capillarity, even if taken together, are insufficient
to raise a fluid to a height of 20 metres. Thus the living elements do not take part in the raising of water within the plant; they may, however, excite "bleeding" by pumping additional fluid into vessels which are already full.

Other striking experiments proved that water can be conducted through stems which have been killed for a great length by immersion in water at a temperature of 90° C. An ascent of liquid took place in spite of the fact that the transpiring organs were at a height of much more than 10 metres above the place of absorption, and separated from it by more than 10 metres of dead stem (p. 647).

Similar results were attained with plants which were completely dead, the only conditions necessary being that the dead tissues should be sufficiently injected with water, and their cell-walls sufficiently saturated (p. 663).

The author further proved that water can be raised by the plant without the help of atmospheric pressure. In these experiments the absorbing plants raised a column of mercury 67 cm. in height (in the case of Dicotyledons), and 70 cm. high, in the case of a Conifer. These mercury columns, with the addition of the column of water in the branch itself, were more than sufficient to counter-balance the atmospheric pressures (p. 791).

This review has already reached an extreme length, and it is impossible to notice the innumerable other points of interest presented by the physiological part of the book. The attention of the reader may however be specially called to the passages on the function of bordered pits (which are particularly adapted to keeping out the air from empty tracheae), on absorption from the soil (in which a qualitative power of choice is again claimed for the roots), and on the function of the tracheae in conducting assimilated food. Here the striking fact is brought forward, that in certain cases of 'ringing' the xylem is able completely to replace the phloem in the conduction of nitrogenous and other organic food-substances to developing organs. This does not, however, affect the fact that under normal conditions this conducting function belongs to the phloem.

In a section on annual rings the author shows that their formation is an inherited character, but that the degree of differentiation between spring- and autumn-wood depends on the intensity of the ascending water-current, for which channels have to be provided, and which acts as a stimulus on the developing cambial cells.
Notice of Book.

It is much to be desired that the present position of the whole question as to the ascent of sap in plants should be brought fully before English readers by some physiologist specially conversant with the subject. In the present review nothing more has been attempted than to point out how complete a revolution in prevailing views must be effected by Professor Strasburger's investigations.

In conclusion it only remains to congratulate the distinguished author on the brilliant success of his latest lines of research, and to recommend his book to the careful study of all botanists, as being the most important contribution of the last fifteen years at once to the anatomy and the physiology of the higher plants.

D. H. S.

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