PATHOLOGICAL PLANT ANATOMY

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by ERNST KÜSTER

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DR. ERNST KÜSTER

Lecturer in Botany in the University at Halle A. S.

Authorized Translation by Frances Dorrance

1913

WITH 121 ILLUSTRATIONS IN THE TEXT

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TRANSLATOR'S NOTE

It is with the deepest gratitude that the translator acknowledges the inestimable assistance of Professors Jones and Humphrey of the University of Wisconsin and their students, Messrs. Yampolsky and Drechsler, who have criticized the manuscript as to technical rendition and general form.

December 1913

Preface

A few years ago in my "Contributions on the Anatomy of Galls", I pointed out the fact, that in judging abnormal plant tissues, not only a comparison of normal and abnormal forms is of great importance but also a comparison of the abnormal with one another, and I mentioned at the time a few abnormal phenbmena, which seemed especially to demand a comparative consideration.

It is intended to give in the present book, a detailed comparative treatment of abnormal plant tissues. I have regarded it as my province to describe briefly their life-history and histology, to study the causes of their production, and to compare them one with another on a basis of ontogenetic, histological and etiological data. I take the liberty herewith of laying the result of these considerations, before the botanical world as the outline of a Pathological Plant Anatomy.

Immediately after my removal from Munich to Halle a. S., I began the necessary experiments in the Botanical Institute here. With great liberality its director, Professor Klebs, placed the abundant resources of the laboratory and the garden at my disposal. For the many favors, by means of which Professor Klebs was always ready to support me in my work, and for much valuable stimulation, I am heartily grateful to my esteemed chief. I owe also, sincere thanks to my publisher, Dr. Fischer in Jena, for his courteous consideration of all my wishes and for the excellent manner in which he has gotten up the book.

Finally I wish to thank the many friends and fellow botanists who have assisted me in my work by sending me experimental matter and literature.

Halle a. S. Botanical Institute of the University

January 1903

E. Küster

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CHAPTER VI

LIST OF ILLUSTRATIONS.

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111, Under Heteroplastic tissues, Read Correlation-heteroplasmas.
p. 1, line 40 - Read in nature for as nature.
p. 2, line 61 - Cormophytes for cormophytes.
p. 7, note 4 - Read uncertain for unsafe.
p. 11, line 18 - Read restrained for sustained.
p. 13, line 2 - Insert semicolon after nucleus.
p. 15, line 3,-Read 1877 for 1887.
p. 19, note 1,-line 8, Read 1882 for 1892.
p. 19, note 2,-line 6, Read XII for XIII.
p. 21, note 4,-line 3, Read 1869 for 1889.
p. 21, line 12,-Read (A) for (a).
p. 23, line 25,- Read composed for exposed.
p. 31, line 2 - Read Kinoplasmatic for kinspessmatons.
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p. 34, note 4 - Change second note 4 to Note 5 and omit Note 5.
p. 40, note 12 - Read medial for denail.
p. 40, note 2,-line 5 - Read CXXXII for CXXII.
p. 42, line 6, - Read Weak for Wak.
p. 42, note 1, line 23 - Read we are for were.
p. 43, note 3, line 15 - Read green and on for gree and one.
p. 45, lines 19-20 - Read Arrested developments for arrestment formations.
p. 47, line 8 - Read an for and.
p. 47, line 13 - Insert numeral 1 for foot-note after greffe.
p. 48, note 1, line 7 - Read between them for between the.
p. 49, line 6 - Read than shade for that shade, omitting comma.
p. 53, line 10 - Read p. 27 for p. 37.
p. 57, note 1 - Read dependence for independence.
p. 58, line 30 - Read Parilla for Barilla.
p. 58, line 37 - protein for albumen.
p. 59, line 1 - Read sulphate and phospate for sulphid and phosphid.
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p. 59, line 45 - Read cells for wells.
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p. 66 - Insert foot notes - 1) Beneke, R. Ein Fall von Osteoid. Chondrosarkom der Harnblase, mit Bemerkungen üb. Metaplasie. Virchow's Arch. f. pathol. Anat. 1900 Bd. CLXI, p. 70, 100. 2) Ziele u. Wege d. Entwickelungsmechanik, 1892. Gesamm. Abhandl., 1895, Bd. II, p. 80 Anm.
p. 68, line 27 - Read divided for divised.
p. 68, line 28, Read Communicating for communicated.
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p. 81, note 1, line 17, Read Bd. L. for Bd. 1.
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p. 91, line 30 - Read hairs for hard.
p. 92, line 16 - Read $CaSO_4$ for CoSO4.

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p. 106, line 30 - Read on for in one another.
p. 110, foot note 3 - Read Remke for Reinke; Pampalone, II. for Pampalone i.e.
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p. 114, line 17, Read are for all.
p. 117, foot note 1, Bd. XIC for Bd. XC.
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p. 130, line 14 - Vöchting for Köchting.
p. 137, line 5 - Insert of after treatment.
p. 138, line 33, - Read if for in.
p. 140, line 10, Read 92 for 82.
p. 142, line 30, Branched for branches.
p. 149, note 2, line omitted after line 5, Landwirtsch. Jahr. 1885, B. XIV, p. 465. Praël Unters.. W, Schutz - u. Kernholz d. Laubbäume.
p. 155, line 35 in the dark for the bark.
p. 161, line 42,-Read mobility for nobility.
p. 161, line 43,- Read tracheid gnarls or balls for tracheid guares on balls.
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p. 173, line 44 - Read of for or contact.
p. 174, line 21 - Read Beyerinck for Bacerinck.
p. 175, line 25 - Read Hymenoptera for Xymenoptera.
p. 177, line 35 - Add asitically after par -.
p. 179, line 29, Read mosses for woods.
p. 180, line 13 - protein for albumen.
p. 188, line 9 - on for or.
p. 189, line 39 - formations for farmentations.
p. 198, line 40 - Omit wound before normal tissue.
p. 202, line 12 - Read contrast for contract.
p. 204, line 30 - Read protein for albumen.
p. 204, line 39 - Read galls for falls.
p. 205, line 12 - Read parenchymatos for parenchymatic.
p. 205, line 14,- Read parenchymatos for parenchymatic.
p. 206, line 4 - ceived for crived.
p. 207, line 4 - Insert etc. after Lasioptera.
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p. 211, line 36 - Read ash gall for ask gall.
p. 212, line 44 - Omit period after politus.
p. 212, line 47 - Read is formed for if formed.
p. 216, line 21 - Read mantel for mental.
p. 217, line 5 - Read lith-like forms for ligh-like forms
p. 219, note 1 - Read (p. 152) for (p. 252).
p. 220, line 6 - Read when the for then the

p. 223, note 2,-line 10, Read p. 289 for p. 269.
p. 226, line 14,-Read which owe for which oo
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p. 257, line 49, - Read -togen for -toeen
p. 258, line 24, - Read forces us for forces as.
p. 258, line 39, - Read ways in for ways ib.

(1) We characterize as abnormal all those forms which deviate from a norm. Since a comparative consideration of different kinds of form-groups leads to the establishment of different kinds of norms, the meaning of the word abnormal will have to vary in accordance with the groups under immediate observation. When studying organisms we have to establish a norm by comparing representatives of a species. This norm will differ from that established in the consideration of greater form-groups. Therefore in speaking of abnormal forms, we will have to define the limitation of the form-groups, to accord with the investigation with which we are then occupied. Botanists commonly consider the growth in thickness of the tree-like Liliaceae, many lianes and so forth, as abnormal because it differs essentially from the growth in thickness in the other phanerogams. In this case the norm has been deducted from a consideration of all phanerogams. If we find double buttercups or fasciated dandelions in the meadow, and plum pockets, cankers, etc. on fruit trees, we term them abnormal formations, because a comparative consideration of the individuals of similar species leads to the establishment of a norm, characterized by single flowers, simple scapes, trees free from canker and so forth. Abnormalities of this kind are also called pathological phenomena or diseases. In this it is assumed, that the functional efficiency of the "abnormal" organism or organs is, in some way and in varying degrees, below that of "normal" ones.

Not all pathological forms found in the plant kingdom are suited for consideration in the manner proposed, only those cases will be discussed in which cells and tissues of abnormal kinds are formed. The comparative treatment of these cases leads to the founding of a "Pathological Plant Anatomy", the characteristic features of which the author has sought to outline in the present work.

(2) Before taking up a detailed consideration to the abundant material furnished by the study of pathological plant tissues, we must first decide whether it is possible to formulate an exact definition for the concept of the "pathological", in contradistinction to the normal.

In my opinion, the efforts of earlier authors to define "pathological", when working with plant diseases, have only proved the impossibility of any sharp division into normal or healthy and abnormal or pathological, as nature. This is as impossible as an exact distinction between the plant and the animal kingdoms. Forms will always be found, of which the true classification remains uncertain. We will not undertake the hopeless task of finding an entirely satisfactory definition; the same difficulties exist also for the relatively limited sphere of our anatomical considerations, that are found in the whole province of pathology. We will only inquire which are the characteristics common at least to the majority of the forms which we, in accordance with general usage, are to designate as pathological.

No useful result whatever is obtained by taking into consideration the histology of abnormal tissues. The anatomical structure of pathological tissues shows the greatest diversity conceivable. This will be fully demonstrated later. No features are found in common. Similar conditions exist in considering their etiology, for the most varied of external conditions may cause the formation of pathological tissue. We obtain useful results only when we take into consideration the <u>physiological</u> peculiarities of the tissues. All the cases which we can designate as pathological in the plant involve the omission or weakening of some function. Either the tissues are retarded in their functional efficiency; that is in their normal formation by some kind

of unfluences. or tissues functionally efficient undergo subsequent changes. In this latter case they lose wholly or in part their ability to function, or new tissues are produced on the plant body of such a nature that the diseased and deformed organs either do not serve the organism as a whole, or at least less than those termed normal. Accordingly, the following tissues among others may be considered as pathological;- the colorless mesophyll of etiolated leaves which through lack of light is kept from developing into functionally efficient tissues, and the assimilatory tissue whose chloroplats degenerate under the influence of external factors, thus rendering the cells incapable of assimilation. Further, new formations like galls, are to be designated as pathological. Their tissues do not serve the organism as a whole, and not infrequently considerable quantities of nutritive material are lost to the organism through their formation. To pathological tissues may be added also wound cork, formed after injury, and "callus" tissue, although the first, by closing the wound, protects the functional efficiency of the organism as a whole, and the second, by a new formation of roots and shoots, has the power of regenerating the original size and efficiency of the mutilated plant body. In
(3) both cases tissues are concerned in whose formation not so much is accomplished for the organism as a whole, as under normal conditions, that is, as would have been produced by the normal tissues of the organism of its integrity had not been destroyed.

Emphasis of the functional characters by which abnormal cells and tissues are distinguished makes possible the rough limitation of the field of our work. Any sharp distinction between the pathological and the normal cannot, however, be carried through in this way. In many cases, the difficulty of judging with certainty of the physiological values of the different tissues would prevent this. A microscopical investigation of their structure does not always enable one to decide as to their physiological significance, and often for technical reasons, the tissues in doubtful cases are not accessible for experimental investigation. In listing definite tissue forms under any one of our chapters, we must be guided by histology and etiology as well as by analogous cases. However, I hope we will not need to deviate from the path indicated by the physiological point of view emphasized above.

The valuation of cells and tissues according to their physiological efficiency reveals the characteristics common to all pathological tissues. When forming groups and sub-groups within the field of our work, it will be advisable to consider ontogenetic and histological points of view as the most important. Therefore, we will unite pathological tissues of similar life history and similar histology and discuss them in independent groups.

Various principles of classification are open to us, we may either describe successively, the individual tissue forms and organs of the plants, and the many variations from the normal structure found in them under certain conditions or we may analyse processes of growth, maturation and differentiation through which abnormal cells and tissues arise, and unite them into independent groups produced by similar processes, without considering which tissue appears changed pathologically, or what organs are involved. In the first case a specialized pathological anatomy would result, in the other case a general one. Since we will have to take into consideration, plants of the most widely different sorts, one-celled as well as many-celled, thallophytes as well as cormophytes, it seems advantageous to me to arrange our material from the point of view of general pathological anatomy. In the concluding chapter there will be opportunity for sketching in outline, a special anatomy, at least for the

If normal individuals of a species are tested for the functional efficiency of all their parts and then those composed partially or entirely of pathological tissue, it will be found that individuals normally constructed attain a maximum of functional efficiency, while that of the others remains more or less below this maximum, no matter what may be the nature of their
(4) variation from the normal histology. Conditions are different, however, if we consider the life history and histology of the cells and tissue instead of their functional efficiency. Cases may be found where individuals constructed abnormally may surpass as well as fall short of the normally developed examples, so far as the number, size, and internal structure of their individual elements are concerned. The normal course of development takes, so to speak, a golden mean from which it can deviate more or less widely in either direction. Proportions of size, number, etc. characteristic for normal tissue, furnish a standard for the fluctuating values to be measured in plants differently diseased.

It is thus evident that a division of the material into two principal groups is advisable for the histological considerations of the subsequent "general pathological plant anatomy":

1. The number, size or differentiation of the cells of pathological tissues remains more or less below the normal. Therefore in one or more ways, the tissues remain in a stage of incomplete development. We designate as Hypoplasia those abnormal processes of formation which - compared with the corresponding normal processes of development - appear retarded as it were and end prematurely.

2. The pathological cells and tissues exceed the conditions of differentiation and growth characteristic of normal individuals. The diversity of forms found to arise through such processes of differentiation and growth necessitates a subdivision into several independent groups.

a. In the simplest case, the abnormal cells differ from normal ones only in their internal structure in the nature of their contents, the character of their membranes, etc. We use the term Metaplasia for the processes of differentiation, by which the cells of any tissue supplement their normal qualities or exchange them for new ones.

b. In other cases, the abnormal cells differ from normal ones in size. Abnormal increase in cell size we term Hypertrophy. It is not fundamentally important whether the histology of the cells concerned remains similar to that of normal ones or is changed in some way.

c. If cell division follows cell growth we speak of Hyperplasia. The number of abnormal formations which comes into existence through hyperplasia is extraordinarily large, and the histological composition of the newly produced tissue is exceedingly varied. Later we will have to undertake a further division of this great group.

Finally there are still to be considered.

3. The Restitution Processes. After injury and mutilation of the plant body, the injured living part often reacts in such a way, that the lost part is formed anew. If the structures arising after mutilation resemble those lost, we speak of restitution. Although the tissues thus produced possess, there-
(5) fore, qualities of the normal ones, they may nevertheless be included in pathological anatomy, since the formation of the regenerated tissues, like that of many pathological tissues, requires an outlay of energy and material which is saved to the plant developing in an undisturbed manner. On account of the correspondence between normal and regenerated tissues, the latter must be the first division of this work.

The processes of differentiation and growth thus briefly characterized lead to the formation of the following five chapters.

I. - Restitution,
II. - Hypoplasia,
III. - Metaplasia,
IV. - Hypertrophy,
V. - Hyperplasia.

In all cases, with words like hyperplasia, etc. we are concerned primarily with the naming of processes. Hyperplasia, for example, is the process leading to the formation of cell outgrowths. However, we will, in the following chapters, take the liberty of designating by the same terms, the actual product of the process of growth or division, etc. The cell outgrowth itself is a hyperplasia,- the abnormally enlarged cell a hypertrophy and so forth. In this we will follow the example of the physician who in the same way uses both abstractly and concretely the terms here named.

The difficulties encountered in defining the whole province are met again when establishing single groups. In many of these we must give up absolutely sharp boundaries. For instance, "hypertrophy and hyperplasia" often merge into one another since, under certain external conditions, in organisms of certain constitution, and in a certain stage of disease, only enlargement of the cells takes place, while in others cell-division may also arise. The few debatable cases in which definite disease-phenomena seem to belong to one chapter or to the other, should not prevent us, however, from leaving both of the groups named to stand independently side by side.

At this point, we must call attention to certain limitations which influence us in the definition of our subject. All pathological structures of cells and tissues should not come under our consideration:- the finer nuclear and protoplasmic structures are excluded first of all. The many results furnished in the past few years by cytological investigation also throw light in part upon abnormal cell and nuclear structures. However, the lack of unity, in judging of normal structural relations, which still prevails even among scientists, seems to prove that the time for a comprehensive consideration of abnormal conditions has not yet come. We will rest content by calling attention incidentally to changes in nuclear and protoplasmic structures, associated with hypertrophy of the cells or hyperplasia, etc. and in conclusion point out some problems and give some bibliographical citations. The further phenomena of degeneration and dissolution so often noticeable in cytoplasm,
(6) nucleus, chromatophores and cell-membrane will be excluded. Some remarks on the phenomena of degeneration may be found in Chapter V. Finally micro-chemical conditions which vary from the normal and are found in pathological cell and tissue forms will be mentioned only incidentally. Irregular reactions of the cell contents and membranes have more to do with abnormal metabolism of diseased plants, than with their pathological tissue structures, the discussion of which is our sole task. For the rest, compare the concluding remarks in Chapter V.

Since in forming groups and sub-groups, we will take pains to place the most natural boundaries possible to the separate divisions of our work, we must consider practicably, besides ontogenetic and histological features of pathological plant tissues, still other distinctive ones. Among these, <u>etiological</u> features are of first importance. In every form of pathological development we will inquire for the causes producing it. The influence upon tissue formation of abnormal supply of light, abnormal nutritive conditions, abnormal water supply, and many others, should be investigated. It will be found that abnormal tissues, which may be traced back etiologically to similar causes often correspond with one another in their structural relations. Therefore it is possible, without forcing matters, to unite a consideration of the etiology with that of the material divided according to ontogenetic and histological characters.

Moreover, most forms of pathological plant tissues and very diverse ones may be traced back to factors other than those abovenamed. They are produced partly by injury, partly by infestation with parasites, animal or plant. All abnormal tissues, arising from "wound stimuli", will be designated as "callus formations" in the widest sense of the word. We will have to speak of callus-hypertrophy, callus-hyperplasia and so forth, according to the way in which the tissues are affected. On the other hand, gall-formation will be spoken of, when parasitic organisms of any kind whatever cause the formation of abnormal cells and tissues. We will report later in detail on gall-hypertrophy, gall-hyperplasia and so forth.

Although a descriptive treatment of pathological plant tissues and a study of their development will especially deepen and broaden our knowledge of the histological development of the plants, yet we will be obliged in considering the etiological side to place above all physiological questions. We will have to test the ways in which various factors affect the plant, and the capacity for reaction of various cells and tissues to certain stimuli; we will be led from the <u>study of forms</u> to the <u>physiology of development</u> especially of a pathological nature. In this way also "pathological plant anatomy" will furnishcontributions to the field, which we will follow Roux in designating as the <u>developmental-mechanics of the organisms</u>.

It will be found that almost all pertinent questions are easily subjected to experimental treatment. The phytopathologist is in the favorable position of being able to produce experimentally the abnormal tissues in which he is interested. In most cases, our knowledge of the factors at work does not ex--
(7) tend beyond the very beginning; indeed there is such urgent need of a thorough further analysis of these factors that the answering of most questions, and indeed the decisive ones, must be held over for future researches.

In each division we will follow the discussion of developmental and histological character by remarks upon etiology and developmental-mechanics. In the concluding chapter, we will recapitulate briefly all that has been ascertained as yet concerning the ways in which the different forces may act.

The subsequent treatment of different abnormal tissue forms will include a series of examples to illustrate each of these forms and attention will be called to the pertinent literature. Of course, it is not in our province to mention all the plants capable of producing abnormal tissues, nor describe all the abnormal structures made known by personal investigation or by the statements of earlier authors. A multiplicity of examples is to be avoided, such as could have been given easily for instance in the chapter on galls. Instead of describing exhaustively all known cases which would be suitable in a manual, we will sift the available material and limit ourselves to depicting those cases important because of a wide-spread distribution, or in any way interesting theoretically. Moreover we have not striven for a complete survey of all the literature concerned with abnormal cells or tissues. Articles will not be named which recapitulate only what is universally known, or which report new facts insufficiently. If, in spite of my endeavors to reproduce all that is essential, important contributions have escaped me, I ask for the forbearance of my reader, in view of the wide range of literature here used.

RESTITUTION

Living plants or plant organs are often stimulated to processes of growth and to the formation of certain kinds of new structures by the violent removal of some already existing part. If this leads to the rebuilding or transformation of organs, different results are conceivable.

1. The newly formed portions arise on the place of amputation and resemble the lost portion in all essential points. If for example, the tip of a root is removed a new root tip will be formed at the place of injury. Decapitated shoots often develop callus on the surface of the cut and from this numerous adventitious shoots; many marine algae proliferate abundantly on the cut surface; other similar examples might be cited.

2. The newly formed portions resemble in all essential points those lost; they are not produced, however, at the place of injury, but at a greater or lesser distance from it. If, for example, we remove from a root not only the tip but also older portions further back, no regeneration takes place as in 1. On the contrary, the cut root is incited to the formation of lateral roots which arise above the place of amputation.

3. The newly formed parts arise on the surface of the cut, but do not resemble the lost parts (heteromorphosis). Cases of this kind arise when, for example, root cuttings of Taraxacum develop leafy shoots on the apical surface of the injury, i. e. on the one toward the root apex, or when seedlings of Bryopsis form rhizoids instead of lost "sprouting parts".

4. The newly formed portions neither resemble those lost nor are they produced on the surface of amputation. Sachs found in the case of Cucurbita that after the removal of all shoot buds, the root buds, present in each leaf axil, developed into knot-like structures. Vöchting[1] recently described his observations on certain species of Brassica, where, after the removal of the vegetative points from all sprouts, he found leaf-cushions trans-
(9) forming in the same way. It should be noticed that the newly formed portions arise from organs already existing, at least in their incipiency.

The processes of regeneration result in a reproduction of the original forms, or structures similar to them can be created, only in the cases named under 1, in which the new parts are produced at the place of injury and resemble those lost in all essential points. Various modifications are still conceivable, however, either the surface of the injury in its entirety takes part in the regeneration, or only portions of it; further, at the place of injury, there arise either one new form alone or several of equal value, near one another. Adventitious shoots of leafy plants, as well as the proliferation of the thallophytes, capable of regeneration, in this process pass first through a stage similar to the "juvenile-forms"; the former with simple leaves, the latter with a cord-like thallus base.

A complete agreement of the lost with the newly formed organ, a <u>restitution ad integrum</u>, will be attained only when the following conditions are fulfilled:-

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[1] Vöchting, Zur experimentellen Anatomie. Nachr. k. Ges. Wiss. Göttingen, 1902. Heft 5.

(a) When the entire injured organ takes part in the regeneration.
(b) When only one new organ arises at the place of injury.
(c) When the appearance of "juvenile-forms", or primitive developmental stages, do not exclude agreement

Processes of restitution, by which an organ is produced entirely similar to the one lost, are rare in the plant kingdom. Roots from which the extreme tips have been removed regenerate the lost part[1]. According to Peters, the tip of the sprout of small Helianthus plants is capable of regeneration[2]. According to Gobel[3] the prothallium of the Polypodiaceae, the pseudo-bulbs of Drepanophyllum and Eriopus, if injured by grazing animals, can likewise regenerate the lost part[4]. The question, whether mutilated leaves are also able to regenerate parts that have been lost, until most recently an open question, has just been affirmatively answered by the experiments of Gobel[5] on Polypodium Heracleum and by Pischinger's[6] on Streptocarpus and Monophyllaea. If finally, we include the new structures on wounded unicellular organisms (Siphoneae), to which we shall return later, then all known forms of true restitution in the plant world will have been named.

(10) Observations similar to these on the restoration of whole organs and organisms may be made on the restitution of cells and tissues. It will be necessary to make investigations in order to see whether the cells, injured by the mutilation of any portion of the plant, are healed by the regeneration of their membrane, their protoplast and so forth, thus regaining their original form or composition:- entirely independent of the question, whether the organism as a whole resumes at the same time its former size and normal form. In the second place, the question must be discussed, whether, after injury, a tissue can be produced from the parts there exposed, which agrees in all particulars with the normal superficial tissues;- in other words, whether, at the place of injury, a normal epidermis or a normal membrane of any kind whatever can be formed, no matter if the reproduction of such tissue is connected with a complete compensation for organs possibly lost.

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[1] Ciesielski, Untersuch. über die Abwärtskrümmungen der Wurzel. Cohn's Beitr. z. Biol. d. Pflanz., 1872, Bd. I, p. 21; Prantl, Untersuch. üb. d. Regeneration d. Vegetationspunktes an Angiospermenwurzeln. Arb. d. Würzburger Institutes, 1874, Bd.I, p. 546. Roots cut in half longitudinally are also capable of regeneration. Compare Lopriore, Ueb. d. Regeneration gespaltener Wurzeln. Nova Acta Ac. Leop. Carol., 1896, Bd. LXVI, p. 233.

[2] Peters, Beitr. z. Kenntnis d. Wundheilung bei Helianthus annuus L. und Polygonum cuspidatum Sieb. u. Zucc. Diss. Göttingen, 1897, p. 109.

[3] Organographis, Bd. I, p. 37; further, Über Regeneration im Pflanzenreich. Biol. Centralbl., 1902, Bd. XXII, p. 385.

[4] Über Regeneration im Pflanzenreich, loc. cit. p. 508. Therein references to unsafe statements on leaf regeneration.

[5] Correns, Untersuch. üb. d. Vermehrung d. Laubmoose, 1899, p. 57, 58, 236.

[6] Ueb. Bau u. Regeneration des Assimilationsapparates von Streptocarpus und Monophyllaea. Sitzungsber. Akad. Wiss. Wien, Math. Naturw. Cl., 1902, Bd. CXI, Abt. I, p. 278.

Plant cells are not capable of living for a long time in an injured condition. After injury to the cell membrane, or after the mutilation of the protoplast, either the cell is destroyed, or changes take place in it, which result in a reproduction of the status quo ante, or of a condition similar to it and of equal value physiologically. These we can designate as healing processes.

The question as to the restitution of the cell-membrane is of the first importance. On the one hand, experimental interference with the integrity of the cell-wall and its connection with the protoplast may be carried out most easily; on the other hand, new cell-membrane formations may usually be proved without difficulty in the object under experimentation. We are thus relatively well informed as to the processes of cell-membrane restitution.

Various kinds of injury must evidently be considered here. We may remove some layers from the cell-membranes without coming in contact with the protoplast itself; we may expose the protoplast by breaking the continuity of its cellulose covering, i. e. by pricking or cutting, or we may loosen the protoplast from its membrane in places, or on all sides, by plasmolysis.

Because of technique, it will be possible to effect the first kind of injury only in cases of unusually strong cell-walls. That the layers which have been torn off can be replaced, has been proved by Tittman[1] with <u>Agave americana</u>, <u>Aloe ligulata</u> and <u>A. sulcata</u>. As is well known, the cuticle on the leaves of these plants is very strongly developed, and may be removed without noticeable damage to the protoplasts. In damp places the newly formed cuticle is weaker than that formed under normal conditions. Tittman observed regeneration of the wax coating on Ricinus communis, <u>Rubus biflorus</u> and <u>Macleva cordata.</u> Various Sedum and Echeveria species lack this capacity for regenerating wax.

(11) Very much greater significance is attached to those cases in which the protoplast in one way or another is exposed partially or on all sides. The effect of injuries of this kind may always be studied experimentally and easily in all cell forms and in all plants. The large celled Siphoneae are especially suitable objects for these experiments, but it will be found that in all the principal groups of the plant kingdom, plants are known in whose cells healing processes may take place after exposure of the protoplast and new membrane formation may be observed. In any case, however, the capacity for regenerating the cell-membrane is very much better developed among the lower plants than among the higher ones.

The experiment, which should throw light upon the conditions of the cell after exposure of the protoplast, is most successful when it is possible to separate the protoplast partially or entirely from its wall, leaving it at the same time unmutilated. Plasmolysis is an excellent condition for obtaining this result.

Klebs[2] has proved that protoplasts can be incited to the formation of new membranes by plasmolytic separation from the

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[1] Beobacht. über Bildung und Regeneration d. Periderms, d. Epidermis, des Wachsüberzuges u. d. Cuticula einiger Gewächse. Pringsheim's Jahrb. f. Wiss. Bot., 1897, Bd. XXX, p. 116.

[2] Beitr. z. Phys. der Pflanzenzelle. Untersuch. d. Bot. Inst. Tübingen, 1888, Bd. II, p. 489.

cell wall. Representatives of the most varied plant groups,- algae (Vaucheria, Zygnema, Mesocarpus, Spirogyra, Oedogonium, Conferva, Chartophora, Stigeoclonium, Cladophora), mosses (Funaria leaves), ferns, (prothallia of gymnograms), and monocotyledonous growths (leaves from Elodea canadensis), furnished results which agreed in all essential points. To be sure, the formation of the new membrane required a varying length of time in different representatives; Vaucheria occasionally formed the new cell covering in 10 per cent glucose within the first hour, Conferva and cells of prothallia after 1 to 2 days, Zygnema needed 3 to 4 days, cells from Funaria and Elodea 8 to 10 days and more. On the other hand it was not possible, by means of plasmolysis in sugar solution, to incite cells of the Desmidiaceae (Desmidium, Euastrum, Cosmarium, Penium, Pleurotaenium, Closterium, Tetmemorus) nor of the Diatoms (Melosira) to the formation of new membranes. Equally without result were the experiments on many prothallia (Blechnum, Ceratopteris), on Lemna and Vallisneria, as well as on dicotyledons (Symphoricarpus). As far as the latter are concerned, the negative result of the experiments may be due to the manner in which they were carried on, as chosen by Klebs, or to the nature of his experimental objects. At all events, his supposition that the capacity for forming new membranes does not extend to dicotyledons generally, is not pertinent in this general conception. The protoplast in root hairs of dicotyledons forms new membranes after the action of plasmolysis. This is true also of the protoplast of pollen tubes[1]. Still further, Townsend found the formation of new membranes in plasmolysed sieve tubes in Bryonia and Cucurbita[2]. Further similar examples will be noted later.

(12) Plasmolysis is known to attain varying degrees, depending upon the nature and concentration of the solution employed; i.e., the protoplasmic membrane may be loosened from the wall only in places or it may be drawn together into a ball, which is separated from the cell-wall on all sides. In the first case only a new cap-like layer is produced, attached on all sides to the old cell-wall which is still in contact with the protoplast; in the second case, a complete sheath is produced around the protoplasmic mass.

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[1] Compare Palla, Beob. üb. Zellhautbildung an des Zellkerns beraubten Protopl. Flora, 1890, Bd. LXXIII, p. 314. Acqua. Contrib. alla conosc. d. cellula veget. Malpighia. 1891, Vol. V, p. 3. The same process takes place "normally" in the cap-formation of the root hairs of the Java-fern Drymoglossum nummularifolium and D. piloselloides (According to Haberlandt, Physiol. Pflanzenanatomie, 2 Aufl. 1896, p. 192): "By longer continued drought, the protoplasm; to wit, of the root hairs which are drying up, together with the cell-nucleus in the basal part of the hair, is drawn back, above which becomes noticeable a more or less regular contraction of the body of the hair. At this point a membrane cap is then formed, which bounds the capsulated protoplast of the hair from the dried up part. The latter drops off and the resulting root-hair base waits only for the resuscitating drop of water in order to grow out at once into a new hair." Reinhardt (Plasmolytische Studien z. Kenntnis des Wachstums der Zellmembran. Festschr. f. Schwendener, 1899, p. 425) has already raised the question, whether the cap formations in the bast, (Krabbe, Beitr. z. Kenntnis der Struktur u. d. Wachstums vegetab. Zellhaute. Pringsheim's Jahrb. f. wiss. Bot., 1887, Bd. XVIII, p. 346) may not also be placed on an equal footing with the above mentioned abnormal formations.

[2] Townsend, Einfl. des Zellkerns auf d. Bildung der Zellhaut. Pringsheim's Jahrb. f. wiss. Bot., 1897, Bd. XXX, p. 484.

More examples may be given for these cases than for those in which, as after plasmolysis, a new formation of the cell-wall takes place after injury to the cells and after violent removal of pieces of cell-wall, with which is connected a simultaneous loss of living cell substance.

In the first place there should be mentioned here also, the much investigated Siphoneae[1], which in part, can heal their wounds even in a very short time by a new formation of cell-wall. All Siphoneae which have been tested, (Anadyonene, Botrydium, Bryopsis, Caulerpa, Codium, Derbesia, Halimeda, Udotea, Valonia, Vaucheria) are capable, without exception, of restoring the cell-wall. The Phycomycetds, which resemble the Siphoneae and which, in forming soar membranes are also protected by the narrow lumen width of their mycelial tubes, act also like the Syphoneae[2].

So far as is known, in almost all cases, the injured cells of higher plants lack the ability of restitution. It is immaterial whether the results of the protoplasmic loss play the chief role, whether the contact of the exposed protoplasm with the external environments acts as a distributing factor, or whether other factors turn the scales:- in any case, the injured cells almost always break down without having healed their cell-walls. As yet only a few exceptions are known.

If the upper part of the nettle hair of Urtica dioioca is broken off, it is immaterial whether only the tip or a larger part be lost - the protoplast now and then forms a delicate scar membrane at a varying distance from the surface of the break. In one case on a mutilated hair, I found a new, very delicate walled tip, not absolutely regular. (Compare figure 1).

Perhaps even regeneration of the tip becomes possible under suitable conditions, so that the same nettle hair may again
(13) become effective as a weapon. Moreover Kallen[3] has already announced, that the hairs of Urtica urens can close their wounds with membranes. It is very possible that the nettle-hair cells of Urtica can also be incited to the formation of membrane caps by means of plasmolysis.

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[1] Of the abundant literature, the following may be named: Hanstein, Ueb. d. Lebensfähigkeit der Vaucheria-Zelle. Sitz. Ber. d. Niederrhein. Ges. Bonn, 1872; Hanstein, Reproduktion und Reduktion von Vaucheria-Zellen. Hanstein's Botan. Abhandl., 1880, Bd. IV, p. 45; Schmitz, Beob. üb. d. vielkernigen Zellen d. Siphonocladiaceen. Festchr. d. naturforsch. Ges. Halle 1879, p. 275; Noll. Ueb. den Einfluss der Lage auf d. Morphol. Ausbildung einiger Siphoneen. Arb. d. Bot. Inst. Würzburg, 1888, Bd. III, p. 466; Wakker, Die Neubildungen an abgeschnittenen Blättern von Caulerpa prolifera. Kon. Akad. Wetensch. Amsterdam, Bd. III, 2. p. 251; Klemm, Ueber Caulerpa prolifera. Flora 1893, Bd. LXXVII, p. 460; Küster, Ueber Vernarbungs-und Proliferations-erschein. bei Meeresalgen. Flora, 1899. Bd. LXXXVI, p. 143; Winkler, Ueber Polarität, Regeneration und Heteromorphose bei Bryopsis. Pringsheim's Jahrb. f. wissenschaftliche Bot. 1900 Bd. XXXV, p. 449; Prowazek, Beitr. z. Protoplasmaphysiologie. Biol. Cbl., 1901, Bd. XXI, p. 87.

[2] Compare especially Van Tieghem, Mouv. rech. s. l. Mucorineens. Ann. Sc. Nat. Bot., 4, ser., Tom. 1, 1875, p. 19.

[3] Das Verhalten d. Protopl. in d. Gew. v. Urtica urens entwicklungsgeschichtlich dargestellt. Flora, 1882, Bd. LXV, p. 65.

The latex tubes may be mentioned as a second example which, after injury, are healed in the same way by the formation of membrane caps. Tison observed the latter in Morus alba and others after the dropping of their leaves[1]. The latex tubes as well as nettle hairs prove again that even the cells of dicotyledons are capable of forming their membranes anew.

If, by injuring the cells, we succeed in exposing the protoplasts on all sides, as described above for plasmolytic processes, we then have a special case, which, however, does not disclose anything essentially new. Through this injury protoplasmic masses of various sizes are often extended from the large cells of the Siphoneae, which given favorable conditions[2], are capable of enclosing themselves with new cell walls.

In this connection it should be noted that many Siphoneae may also heal their wounds in other ways than by reforming the cell walls. If a turgid cell of Valonia utricularis be pricked, a fine stream jets forth. When, however, the jetting of the liquid is sustained by a gentle finger pressure, it soon ceases and a gall-like protoplasmic plug free from chlorophyll, which closes the wound, is formed at the prick point. Later the formation of a new piece of membrane follows this provisional ligature. In the case of strong sacs of Bryopsis, after injury and the resulting ejection of protoplasmic fragments, a plug of a granular substance is formed which I consider disorganized pro-
(14) toplasm[3]. The formation of these peculiar stoppage masses in injured cells may be followed under the microscope. The production of the granular mass gives an appearance similar to that formed by the hardening of a drop of wax. Sometimes crystals of perceptible size are formed in this stoppage mass, the growth of which may be followed satisfactorily under the microscope, although all the processes here described take place in the fraction of a minute. The latex tubes are also closed after injury by coagulation plugs.

Among the scar-membranes formed after plasmolysis or after injury, we find some which entirely resemble normal ones in structure and capacity of growth, and still others, showing some variations, as, for example, in the above mentioned scar-membrane of Urtica, which remains very delicate and, more noticeably in Algae, in whose cells Klebs found that soft, weakly refractive membranes, obviously very rich in water, were produced after plasmolysis. (Spirogyra, Mesocarpus). Presumably, the action of the foreign medium surrounding the cell (10 to 15 per cent sugar solution) lies at the bottom of this.

It should be observed still further that all the newly formed membranes are not capable of growth. While in many Siphoneae, it may be demonstrated that scar-membranes often make a prolific surface growth soon after their formation, still in the case of cell-walls of other plants formed after plasmolysis, this growth is regularly lacking, for example, in the cells of Elodea or Funaria as cited by Klebs. In the plasmolysed and newly enclosed cells of Oedogonium, no growth takes place, only division and the formation of swarm spores. Where growth results, it leads in many

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[1] Rech. s. la chute d. feuilles chez les Dicot. These, Caen 1900.

[2] Compare Klebs and Schmitz in place mentioned. Further Haberlandt, Ueb. die Lage des Kerns in sich entwickelnden Pflanzenzellen, Ber. d. D. Bot. Ges. 1887, Bd. V, p. 211 and others.

[3] Compare Küster, Ueb. Derbesia and Bryopsis. Ber. d. D. Bot. Ges. 1899, Bd. XVII, p. 77.

cases to the development of abnormal types. In the case of Zygnema, as described by Klebs, irregular, spirally twisted structures are produced. (Compare figure 2). I found that growth of the scar-membrane of Anadyomene in aquarium culture, always leads to abnormal rhizoid-like forms. Undoubtedly in both cases the abnormal activity of the growth may, under suitable culture-conditions, be replaced by normal formative processes

Finally those conditions are still to be discussed, the fulfillment of which must be considered as taken for granted in the processes of restitution already described.

Experiments with protozoa have proved that isolated cytoplasm can form no new nucleus from its own substance and that isolated nuclei are just as little able to form cytoplasm. The regeneration of the cytoplasm presupposes a fragment of cytoplasm, the regeneration of the nucleus, a fragment of the nucleus. Further - regeneration of the cytoplasmic bodies from a remnant of cytoplasm can take place only when a nucleus, or a fragment of a nucleus, remains connected with it and, conversely, a nuclear fragment can be restored to a normal nucleus, only when the cy-
(15) toplasm, or a remnant of it, remains attached to this fragment. Isolated nuclei without cytoplasm and cytoplasmic masses without nuclei are incapable of living for any length of time[1]. At least parts of cytoplasm and nuclei must remain united, if there is to be any restitution of the cell.

These interrelationships were first observed in protozoa, whose large, easily dissectable nuclei make them favorable objects for experimentation[2], but for a long time they were misconstrued, inasmuch as the activities of the nucleus, the "element of the cell which bears the inheritable characters and qualities", were considered as the alpha and omega of all regeneration processes, and the importance of the cytoplasm completely overlooked[3].

It is evident, from what has been said above, that the wall so important for plant cells, can be regenerated also on cell fragments which lack it entirely, and that further, its new formation is produced from the cytoplasm. The fact that the cytoplasm can build a new wall only in the presence of and under the influence of the nucleus is important here. Schmitz was the first to prove that isolated cytoplasmic fragments from cells of the multi-nucleated Siphonocladiaceae can remain capable of life and of forming new independent cells, i. e. can provide themselves with a new wall, only if the severed cytoplasmic mass has taken

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1 Compare Verworn, Physiol. Bedeutung des Zellkerns. Pflüger's Archiv. 1891, Bd. LI, p. 1.

2 The first experiments originated with Nussbaum (Ueb. spontane und Künstliche Teilung. Sitz.-Ber. d. Niederrh. Ges., Bonn 1884, Ueb. d. Teilbarkeit der lebendigen Materie. Arch. f. mikr. Anat. 1886, Bd. XXVI, p. 485) and Gruber (Ueb. künstl. Teilung bei Infusorien I and II. Biol. Cbl., 1884, Bd. IV, p. 717 and 1885, Bd. V, p. 137, Beitr. zur Kenntnis der Phys. u. Biol. der Protozoen. Ber. d. Naturforsch. Ges. Freiburg, 1886, Bd. 1, 2).

3 Compare especially Verworn, Allgem. Physiologie, 1895, p. 486 ff. Theoretical discussions, on the significance of the nucleus by Loeb. Warum ist die Regeneration kernloser Protoplasmastücke unmöglich oder erschwert? Arch. f. Entw.-Mech., 1899, Bd. VIII, p. 689.

with it one or more nuclei from the mother cell. Klebs[1] has treated in detail the significance of the nucleus enucleated cytoplasmic pieces from the cells of Zygaema, Spirogyra and Oedogonium, or of Funaria, remained living a long time, to be sure, in cane-sugar solution and, in the case of Spirogyra and Zygnema, formed starch in their chromatophores, but never walls. Haberlandt's experiments[2] continue those of Schmitz and Klebs, and give the same results. According to Prowazek (loc. cit) the greater the number of nuclei contained by the cytoplasmic mass, the more quickly these regenerate[3]. The theory brought forward by Palla (loc. cit.) that cytoplasmic pieces without nuclei are also capable of forming cell-walls has been disproved by the work of Acqua and Townsend (loc. cit.).

(16) The last named author took an important step forward when he discovered the distant effect of the nucleus. Even pieces of cytoplasm free from nuclei are capable of forming membranes if the influence of the nucleus can be extended to them by means of connecting strands from distant portions containing nuclei or from uninjured cells lying at a distance. In this, however, a "living continuity" is necessary, contact alone being insufficient for the transference of this influence. The best data on the influence carried from cell to cell is given by the experiments with sieve tubes of Cucurbita and Bryonia which lack nuclei, but which may form new walls after plasmolysis. In no case could the formation of membranes be observed in the completely isolated, cytoplasmio masses of the sieve tubes which had passed out of the tubes. Townsend proved the transmission under the influence of neighboring cells containing nuclei, of the wall-forming stimulus to a distance of several millimeters under the influence of neighboring cells containing nuclei[4].

Nothing is known as yet of any after effect of the nucleus

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[1] Compare Tagebl. der Berliner Naturf.-Vers., 1886, p. 194; Ueb. d. Einfluss d. Kernes in der Zelle. Biol. Cbl. 1887, Bd. VII, p. 161; Beitr. z. Phys. d. Pflanzenzelle. Ber. d. D. Bot. Ges., 1887, Bd. V, p. 181; further the detailed publication already quoted.

[2] Besides the above quoted articles compare, Ueb. d. Bezieh. zw. Funktion and Lage des Zellkernes b. D. Pfl. 1887; Ueb. Einkapselung des Protoplasmas mit Rucksicht auf d. Funktion des Zellkernes. Sitz.-Ber. Akad. Wiss. Wien, math.-naturw. Kl., 1889, Bd. XCVIII, Abt. 1, p. 190.

[3] Gruber, (loc. cit.) states, that pieces of protozoa reform complete bodies the more quickly, the larger the nuclear fragment, which they have carried with them.

[4] By this distant reaction of the nucleus the above quoted observations of Palla (loc. cit.) may well be explained, as well as those of A. Grüttner, Ueb. die Erzeugung von kernlosen Zellen etc., (Diss. Erlangen, 1897). Strumpf tried in another way to harmonize the different results with one another; he expresses the conjecture that the cytoplasm of young cells, even without nuclei, may form membranes, but that the old cells need the reaction of the nucleus. (Zur Histologie der Kiefer. Anz. Akad. Wiss. Krakau, 1898, p. 312).

upon enucleated pieces of cell[1].

Scar membranes occur in most plants of which the cytoplasm is found capable of forming them[2], so far as the above described action of the nucleus is made possible. In some other plants it appears that the conditions for wall-formation are not yet exhausted with this; at least, according to Klebs, in plasmolyzed cells of Zygnema the influence of light is a further condition for wall-formation.

We have spoken as yet only of the restitution of the wall. Unfortunately, we are imperfectly informed as to the regeneration of the living cell elements. The fact that mutilated cells, whose wounds have been healed by a new formation of membrane, can continue growth has been emphasized for different kinds of plants. Since the cells during and after growth contain normal protoplasmic quantities,- so far as an estimate allows of any decision, it may be accepted that the mutilated protoplasmic body is capable of a restitutionary growth. Nothing has yet been learned as to whether nuclear fragments, as in the case of
(17) protozoa, can also grow into normal nuclei, whether mutilated chromatophores, as those of the conjugates, can attain their normal size by growth, whether in mature assimilatory cells, after the removal of some protoplasm and chlorophyll body, all that remains in the cell can be excited to division;- and much more of the same kind.

2. RESTITUTION OF THE TISSUES

In the following, those processes of restitution will be discussed, in which the injured cells themselves are not healed, but in which intact cells near the injured ones make reparation by growth, eventually also by division. At least two cells will therefore take part in the whole process, the one injured and the one making restitution.

This, the simplest case, is realized in the liverworts; for example, in Marchantia. If the long, unicellular rhizoids are cut off from youthful parts of the thallus, compensatory hairs are formed, even after a few days, one of the neighboring cells of the trichome base (compare figure 3a) developes into an unicellular hair. The compensatory hair grows out through the cavity of the mutilated one, and from the end of the stump, into the substratum. The lumen of this substitute hair is often noticeably narrower than that of the normal hair.

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[1] Gruber, (Beitr. z. Kenntnis d. Phyz. u. Biol. d. Protozoen in place mentioned p. 13) states that in fragments of protozoa, lacking nucleus, incomplete peristomic regions may still develop as a result of an after effect of the nucleus. According to Balbiana (Nouv. rech. expér. sur la mérôtomie des infus. ciliées Arch.de Microgr. 1891/1892, T. IV, p. 369) an after effect can be demonstrated only in so far, that a constriction is found in those nucleus-free pieces of individuals, which were taken directly before their cell-division. Never, however, does complete cell-division take place; on the contrary, the two halves fuse again.

[2] To be sure, there are exceptional cases, in which even in the dark (Klebs loc. cit., p. 541) "a formation of cell walls takes place about the spherical protoplasts. In pure sugar solutions I have observed this very rarely, while, on the contrary, in sugar congo red, a number of protoplasts in each larger culture of Zygnema C. were surrounded with a red cell-wall".

Diaphyses of this kind were thoroughly described for Marchantia and Lunularia by Kny[1]. Since my experiments have proved that any desired number of compensatory structures may be called forth by cutting back the rhizoids, this development of the parenchyma cells on the trichome base may be brought into undoubted connection with the wound stimulus or its results. To conclude from Kny's data, other factors also seem able to excite a stimulus, similar to the one usually associated with the nutilation of the rhizoid. At least Kny states that diaphyses occur also in rhizoids in which the membrane is intact. Then the secondary hairs find at the tip of the primary ones an energetic opposition to further elongation, which may lead to a bending and curling.
(18) Kny observed further that even a tertiary hair may develop in a secondary (Fig. 3b) and that, occasionally, two cells at the base of the primary rhizoid, instead of one, may develop into compensatory hairs.

In the case of many multicellular algae, the thallus of which is made up of filaments consisting of rows of simple cells, (for example, Trentepohlia) similar regeneration phenomena take place after the removal of the growing tip. The uppermost cell, left intact, continues the growth of the mutilated filament. Therefore, the regenerating phenomena of growth proceeds here also from one cell[2].

In the case of the higher plants, restitution processes of this, the simplest kind, are rare. The processes of healing and regeneration observed by Miehe on Tradescantia virginica are somewhat comparable to the diaphyses of Marchantia rhizoids. After the dying off of single epidermal cells, or small cell groups, the wound is closed over by the growth of the intact neighboring cells. In this way, one may occasionally find single cells completely filling out the gap of the dead neighboring elements. I will return later to these phenomena. (Chapter IV, 4).

Regeneration of tissues, brought about by unlimited division of the exposed cells, often takes place in thallophytes in so far as a differentiation of pith and bark tissue may be recognized in them.

In the sclerotia of Coprinus stercorarius, investigated by Brefeld, the outer coat consists of six to eight layers, with black cuticularized walls. If these are removed, the inner cells regenerate a new outer coat. "Some division in the inner cells, as well as the very close association of the cells which have divided to produce the thinner tissue of the outer coat together with a stretching of the outermost cell-layers to form the great cells of this coat are the processes, which must necessarily take place, in order to develop the outer coat from the inner cells".[3] This experiment may be repeated with sclerotia, as long as the inner substance lasts.

Algae, especially the Florideae, behave similarly in the extent to which they exhibit tissue with distinguishable pith and bark. By truncations and tears, or after removal of the bark, a

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1 Eigentüml. Durchwachsungen an den Wurzelhaaren zweier Marchantiaceen. Verh. Bot. Ver. Prov. Brandenburg, 1880, Bd. XXI, p. 2.

2 Illustrations in de Wildeman: Sur la réparation chez quelques algues. Mém. cour. et autres mem. acad. Belgique, 1899, T. LVIII.

3 Brefeld, Botanische Untersuch. über Schimmelpilze. 1887, Bd. III, p. 25.

small-celled bark, rich in chromatophores, is regenerated from the large, colorless or slightly colored cells of the pith. According to Massart[1] some brown algae (Laminaria, Pelvetia) also behave in this way; in them a small celled soar-tissue is also produced from the exposed inner layers, which resembles the hormal bark tissue.

Only a few cases of tissue restitution are known in the high-
(19) er plants. The periderm is on the whole easily regenerated,[2] the epidermis, however, not always. Although in "physiological" injuries, by means of which perforated or secreted leaves of different plants obtain their characteristic form, a tissue is formed at the edge of the wound, which corresponds with the epidermis[3], yet when the integrity of the stems and the leaves is violently distrubed generally no new formation of the epidermis takes place. Tittman has proved this definitely by countless experiments. According to Massart (loc. cit. p. 55) the leaves of Lysimachia vulgaria seemingly form an exception to the rule; they regenerate normal hair-bearing epidermis, when injured in a very young stage. In roots, the ability to form new epidermis after injury is widespread; Lopriore[4] observed on split roots the formation of normal epidermis provided with root hairs. (Compare fig. 4). In the formation of lateral roots also a typical epidermis arises from the derivatives of the more deeply lying layers of tissue.

Finally the regeneration of the vascular bundles is to be mentioned. Roots and shoots which have been split lengthwise will complete each half of the fibro-vascular system to a complete cen-
(20) tral cylinder[5]. In monocotyledons, regeneration of roots takes place by the simultaneous restoration of epidermis, phloem and xylem. In dicotyledons, however, the endodermis is regenerated first, later the xylem and phloem (Compare again fig. 4). In the same way, after splitting shoots of Salix, Aristolochia, Lonicera, Sambucus and many others, Kny observed the production of wound tissue from pith, cambium and bark, in which a new cambium was formed. This was connected on both sides with the cambium of the normal vascular-bundle, and, like this, produced xylem elements towards the inner phloem elements towards the outer side. The investigations of Kny and Lopriore make it probable that very many, if not all, phanerogams possess the ability to restore destroyed central cylinders.

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[1] Massart, La cicatrisation chez l. veg. Mem. Cour. et autres, mem. Acad. So. Belgique, 1898. T. LVII.

[2] Tittmann, loc. cit. p. 117.

[3] Schwarz, Fr., Über die Entstehung der Löchar and Einbuchtungen an dem Blatt von Philodendron pertusum. Sitzungsber. Akad. Wissensch. Wien, 1878, Bd. LXXVII, Abt. 1, p. 367; Lippitsch, Ueber das Einreissen der Laubblätter der Musaceen and einiger verwandter Pflanzen. Oest. Bot. Zeitschr., 1889, Bd. XXXIX, p. 206.

[4] Uber Regeneration gespaltener Wurzeln, loc. cit. Compare also Ber. D. Deutsch. Bot. Ges., 1892, Bd. X, p. 76.

[5] Compare especially Kny, Ueber künstliche Verdoppelung des Leitbündelkreises im Stamme der Dikotyl. Sitzungsber. Naturf. Fr. Berlin, 1877, p. 189. Lopriore, loc.cit. and Vorlaufige Mitteilung über die Regeneration gespaltener Stammspitzen. Ber. der Deutsch. bot. Ges., 1895, Bd. XIII, p. 410.

CHAPTER II

HYPOPLASIA

21

We speak of Hypoplasia if an organism or one of its parts does not attain a normal development but ends its development prematurely, so that forms or characteristics appear fixed as final, which, under normal conditions, belong only transitorily to the organisms or organs concerned. To put it briefly, Hypoplasia is defective development, and its products remain in one or in several respects below the results of normal development. The development of the organisms or organs appears as though "arrested", on which account we can term the products of a hypoplastic process <u>arrested developments</u>.[1] From the aforesaid it follows that in treating of arrested developments, we will be concerned only with forms and pecularities of the organisms and thier parts, already known from the ontogeny pf normal individuals.

The discussion of arrested-development devolves upon either morphologists or anatomists, according to whether the arrestment may be recognized in the maturing of whole organs, or in the development of the cells and tissues. On the morphological side a large number of obsgrvations have been collected and utilized scientifically.[2] They prove that the arrested development of similar organs can result very differently, since very different stages of the normal progress of development appear to be "fixed". In addition to this, it is proved that those processes of growth and differentiation are not always equally arrested, which in a normal course of development, are associated in time and place. Thus, for example, very different kinds of arrested-developments may be pointed out in leaves. In many such cases,
22 the leaves vary from those normally developed in the smallness of their size. The etiolated sprouts of many plants furnish examples of this. In other cases the leaves are less retarded in size than in form; for example, in the case of specimens of Sagittaria grown under water, of the Retinospora form of many conifers, different galls on the tips of the shoots, etc. Thirdly, the form of the leaf may remain undeveloped. Either the initial folding and curling of the leaf blade is retained, as in the artificially forced branches of Aesculus, Gingko, etc.; in the etiolated specimens of Viola; in many leaf galls (Phytoptus mites on Rosa, Fagus, etc.); or the inclination of the leaf to the axis remains as it was at first,- for instance, in willow leaves unfolded under water, in the galls on the tips of Glechom shoots (Cecidomyia), etc. Of course the leaves may also "remain below the normal" in more than one respect. The examples here chosen should demonstrate at the same time that arrested developments of the same character can be produced by the most varied influences.

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1. The word <u>Hypolasia</u> is derived from the terminology of the medical science; the term <u>arrested development</u> has long been familiar to botanists.

2. Compare especially Gobel, Organographie, 1898, p. 121, and the literature quoted therein.

The diversity manifested in the arrestment of cell and of tissue development is very similar. Either the number of the cells composing a certain organ or forming a certain definite tissue, remain below the normal, or the size of the individual cells is smaller than under normal conditions, or finally, the internal structure of the cells and the differentiation of the tissues stops at a primitive stage. Hence the succeeding elaborations follow without further discussion.

Arrested developments of the most varied kinds are to be observed abundantly, on the one hand, in many plants in nature, or on the other hand, may be readily called forth by experimental interference at any time. Since, furthermore, arrested development of cells and tissues is often combined with some obvious external characteristics, the attention of the botanist has been repeatedly directed to them. Correspondingly, a surprisingly large number of reports may be found in the literature bearing upon the same abnormal conditions. On account of the often very inadequate content of the works, it will be sufficient to mention only selected ones in the discussion which follows.

A. NUMBER OF CELLS.

We have spoken already of arrested developments, in which the bulk of whole organisms or single organs remained below the normal proportions. In so-called Nanism, that is, when the plants attain only a fifth or a tenth of their normal size as a result of continued drought or unfavorable nutrition, a corresponding reduction of the size of the cells to a fifth or a tenth of their normal proportions does not take place parallel to the reduction of the plant volume; on the contrary, the cells of the dwarf specimens consist
(23) essentially of cells approximately as large as those of normal individuals; the small size of the starved individuals being chiefly brought about by a reduction in the number of cells.[1]

Similar conditions exist if only single organs, leaves, blossoms, fruits, and not entire plants are dwarfed. For our histological consideration, however, in both cases, only those come into question in which decrease in the number of cells in connection with a shortening of the internodes, a reduction of the leaf-blade, etc. brings about a variation in the histology of the organs concerned. Such cases exist, for example, if the number of the cell layers in the mesophyll decreases, if, by the disappearance of one or more palisade layers, the proportion between palisade and spongy parenchyma

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1. Compare for instance, Möller, H., Beitr. zur Kenntnis der Verzwergung (Nanismus). Landwirtschaftl. Jahrb., 1884, Bd. XIII, p. 167 and especially Gauchery, Rec. sur le nanisme vegetal. Ann. Soc. Nat. Bot., VIII, serie, T. IX, 1899, p. 61. (Further literature is quoted therein.)

is changed, and so forth. Some histological variations of this kind are to be discussed in the following.

1. The structure of the leaf tissue is dependent, to a high degree, on the action of external factors, the number of cell-layers which form the mesophyll and epidermal tissues varies with the life conditions of the plant. The difference between
(24) the leaves of many plants exposed to the rays of light and those grown in shade, verified by Stahl and other authors, is well-known[1]. In the mesophyll of the sun leaves of Fagus silvatica (compare fig. 5 b.) six to eight or even more cell layers lie one above the other,- in the shade leaves only three (fig. 5c). With the medium supply of light, the development of the mesophyll keeps the mean, (fig. 5a). This arrestment, due to insufficient exposure to light, is undergone also by the mesophyll of other plants, further by the epidermis of those plants, which normally develop a many-layered upper covering. Figure 8 demonstrates the difference between the epidermis of a sun leaf, and a shade leaf of Ficus stipulata; the cross divisions are lacking in the leaf kept in shade. We will return later to other differences between shade and sun leaves.

The characteristic development of shade and sun leaves is determined less by light itself than by transpiration, which proceeds in the latter much more actively than in the former. On this account, leaves with the scantily developed mesophyll of shade leaves may be produced in damp air with an abundant supply of light[2].

Griffon[3] verified the reduction of the number of layers in Canna, Chrysanthemum and others, in his comparison of the pale green varieties with those normally green.

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[1] Compare especially Stahl, Ueber den Einfluss der Lichtintensitat auf Struktur und Anordnung des Assimilationsparenchyms. Bot. Zeitung, 1880, Bd. XXXVIII, p. 868. Ueber den Einfluss des sonnigen und schattigen Standortes auf die Ausbildung der Laubblätter. Jenaische Zeitschr. f. Naturwissenschaften, 1883, Bd. XVI. Further, Pick, Ueber den Einfluss des Lichtes auf die Gestalt und Orientierung der Zellen des Assimilationsgewebes. Botan. Centrabl. 1892, Bd. XI, p. 400; Haberlandt, Physiol. Pflanzenanatomie, 2. Aufl. 1896, p. 252. (More literature references therein). Compare also the literature quoted on the following pages.

[2] Compare the experiments of Lothelier, Rech. sur les pl. a piquants. Rev. gen. de Bot., 1893, T. V. p. 480; further Vesque, Sur les causes et sur les limites des variations de structure des vegetaux. Ann. Agron., 1884, T. IX and X. Vesque et Viet. De l'infl. due milleu sur la struct. anat. des. vegetaux. Ann. Sc. Nat. Bot., VI. serie, T. XIII, 1881, p. 167.

[3] L'assimilation chlorophyllienne et la coloration, Ann. Sc. Nat. Bot., VIII, serie, T. X. 1889, p. 1.

This dependence on external factors, as shown in mesophyll and epidermis, in reference to the number of cells and layers, is proved also in the multicellular hairs of many plants, the tissues of the bark, and still others,- and always in the sense that with decreased transpiration fewer cells and cell layers are formed than under normal conditions:-[1]

2. The reduction of the cell number in the products of the cambium is very striking. The varying amount of the annual increase of our trees is well known, its dependence upon external factors having been proved by research. Factors acting locally re involved if the growth activity of the
(25) cambium is retarded by strong pressure,[2], or if the increase in growth continuously remains less on the windy side than on the opposite one.[3] The effect of disturbances in nutrition or that of unfavorable climatic life conditions, is expressed equally in all parts.[4] In the far north or in an Alpine climate the activity of growth of the cambial ring is always less than in lower altitudes or temperate latitudes.[5] Oger observed this arrestement in plants kept

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1. Mitteilungen über das Blattegewebe einiger Moose (Reduktion der Lamellen bei Feuchtkultur) in Gobal, Organographie, p. 364.

2. Küster, Ueber Stammverwachsungen. Pringsheim's Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 487.

3. Hartig, R. Wachstumsuntersuchungen an Fichten. Forstl.- Naturwissensch. Zeitschr., 1896, Bd. V, p. 1. Compare also Busgan Bau und Leben unserer Waldbaume, Jena 1897, p. 98, 99, and the literature quoted therein.(Schweinfurth and others.)

4. Hartig, loc. cit. also Zeitschr. f. Forstl- und Jagdwesen, 1871, Bd. III, p. 340 (Holzuntersuch., 1901, p. 5) and other places.

5. Lazniewski, Beitr. z. Biol. der Alpenflanzen. Flora, 1896, Bd. LXXXII, p. 224. Kraus, Bemerkungen üb. Alter- u. Wachstumsverh. ostgrönländischer Holzgewächse. II. Deutsche Nordpolfahrt, 1874. Kihlman, Pflanzenbiol. Studien aus Russisch-Lappland. Acta Soc. F. et Fl. Fennica, T. VI, Nr. 3. Helsingfors 1890. In Pinus silvestris, H. Hoffman observed an abnormal lobated wood-body which was produced by local arrestment of the formation of xylem. (Ueber abnormale Holzbildung. Centrabl. f. ges. Fortwesen, 1878, p. 612; Compare Just, Jahresber., 1878, Bd. VI, 2, p. 1187).

very dry,[1] etc. The cork meristem also acts like the cambium. According to Douliot it is less active on the shaded side of the branch than on that exposed to light.[2]

It is not surprising that the growth activity of the cambial ring not only loses its normal intensity by continued and sufficiently intensive action of the disturbing factors, but also in places comes temporarily to a complete standstill. As a matter of course we do not need to repeat the fact that each process of growth presupposes a minimum of heat supply, nutrition, etc. We will call attention only to a few cases in which the interruption of the normal processes of growth brings about variations in the histology of the plants or of parts of them. Unfavorable conditions of light and nutrition retard in places the setting of the cambial activity.[3] or can bring it to a standstill for a number of years, or even permanently. Weak spruces discontinue their growth in thickness in the lower parts of the trunk; the brambles behave similarly.[4] Mer (loc. cit.) observed on hyponastic conifer branches that the normal growth in thickness progressed only in a longitudinal half, and thus led to the formation of half of an annual ring. How far "normal" life conditions and
(26) "normal" phenomona of growth are involved in the production of semi-annual rings is an open question.[5] Finally, even factors with a narrowly

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1. Oger, Etude, exper. de l'action de l'humid, du sol sur la struct. de la tige et d. feuilles. C. R. Acad. Sc. Paris, 1892, T. CXV, p. 525. Further references on reduced cambium activity are to be found in the treatises quoted on page 26, ff.

2. Douliot, Rech. sur la periderme. Ann. Sc. Nat. Bot. serie VII, T. X, 1889, p. 325; Infl. de la lum. sur la devel. du leige. Journ. de Bot. 1889,T. III,p. 121.

3. Hartig. Untersuchungen ub. die Entstehung u.d. Eigenschaft des Eichenholzes. Forstl.-Naturw. Zeitschr. 1884, Bd. III, p. 1, Mer, sur les causes de variation de la densite des bois. Bull.Soc. Bot. France,1892, Tom.XXXIX p. 95, etc.

4. Hartig, Das Aussetzen der Jahresringe bei unterdruckten Stammen. Zeitschrift f. Forst - und Jagdwesen, 1889, Bd. I, p. 471. Ueber den Entwickelungsgang der Fichte im geschlossenen Bestande nach Hohe, Form und Inhalt. Forstl Nturw. Zeitschr. 1892, Bd., I, p. 169, etc.

5. Compare also Lammermayr, Beitrage z. Kenntniss der Heterotrophie v. Holz. u. Rinde. Sitzungsber, Akad. Wiss, Wein, math-naturw. Klasse, 1901, Bd. CX.

limited field of action may in places arrest growth in thickness, such as strong pressure (Kuster, loc. cit.) disturbances in nutrition due to parasites, etc.[1]

In conclusion, still a reference to dwarf forms, the anatomy of which Gaucher (loc. cit.) has described in detail. According to his observations, the scanty development of the secondary tissues or their complete absence may be added to the constant histological characteristics of dwarf forms. In many cases no meristematic zone whatever is demonstrable between xylem and phloem, in others a cambium appears, which develops, however, only a moderate activity. Figure 6 makes very clear the difference between a normal stem (a) and a dwarfed one (B) of Erigeron canadensis. Between the two extremes here shown, all transitonal forms with more or less well developed secondary tissues are possible.

As a matter of course, in the present discussion, only a limited number of examples is given, which might easily have been increased. A continuation of their enumeration would give, however, no new points of view, and may well be abandoned. For the rest, the literature quoted in the succeeding divisions cites numerous other examples of hypoplastic decrease of the cell number.

27

B. SIZE OF THE CELLS

As may be supposed from the very beginning, abnormally small cells,- when considered ontogenetically may be produced in different ways:

They may divide anew, before they have reached the size which the cells under normal conditions usually have when ready to divide. No law exists which would bring cell division into compulsory dependence upon a definite cell-size. This method of production plays an especial part in the case of lower organisms which increase by division. Or the growth in length following the last cell division, is either omitted or ends prematurely; or the cells end the course of their development prematurely, so that all the processes of growth and division are lacking, which under normal development would still have taken place in them.

In the following description it will prove advisable not to take as a basis developmental differences in the distribution of materials, but to describe in order the phenomena of arrestment in different organisms and kinds of tissue. We will begin therefore, with an example of the first-named mode of development.

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1. Brunchorst, Nogle norske shovsygdomme. Bergens Mus. Aarbog. 1892.- Just. Jahresbericht, Bd. XXIa, p. 438, (einseitige nach Infektion met Peridermium Pini). Mer, Le chaudron du sapin. Rev. gen. de Bot., 1894, T. VI, p. 153.

In his "Contributions to the Biology of the Plant Cell" Klebs[1] describes a singular observation on Eustrum verrucosum. These Algae were cultivated in a 10 per cent cane sugar solution. No Plasmolysis took place; on the contrary, the cells began to divide, whereby active growth was so hindered that the daughter cells divided anew before they had attained their normal form; the next generation did the same. Thus, not only abnormally formed cells were produced which varied greatly from the type of the species (compare fig. 7a), but dwarf specimens also, appreciably smaller than their normal progenitors and living only a short time (compare fig. 7b). The theory that some form of arrestment exists here is justifiable, since the growth activity of the single cell ends prematurely, resulting in abnormally small individuals.[2]

In higher plants, when hypoplasia is shown by the production of abnormally small cells, the conditions are gen-
(28) erally such that the period of elongation, which under normal conditions, would follow the last cell-division either does not take place or ends prematurely.

Of course it is impossible to differentiate sharply between arrested developments of this kind and "normally" developed tissues. Some tissues, as for example, the palisade parenchyma of many leaves and the cork and the primary bark of some woody plants are exposed of cells of nearly equal size. In other tissues, such as the endodermis of Fiscus elastica and the xylem of many woody plants, the volume of elements of equal value physiologically and histologically, fluctuates within wide boundaries. Hartig and Sanio [3] have proved for tracheal tubes, tracheids, and wood fibres of various trees, that their size is not only dependednt upon the season in which they are produced as shown by a study of the annual rings, but that in various annual growths, at varying heights in trees, etc. elements of regularly varying size may be met with.Since, in spite of all differences in normal individuals a constant average

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1. Tubinger Untersuchungen, 1888, Bd.II,3,p. 547.

2. It is to similar factors that also the "bastard form" belonging to the genus Euastrum and described by Bennet, may well owe its production. Ann. of Bot. 1889, Vol. IV. 171.

3. Hartig, Th. Vollstandige Naturgeschichte d. forstl. Kulturpflanzen Deutschlands, 1851, p. 207. Sanio, Vergleich. Untersuchungen uber die Elementarogane des Holzkorpers. Bot. Zeit. 1863, Bd. XXI, p. 128; Vergleich, Untersuchungen uber die Elementarogane des Holzkorpers. Bot. Zeit. 1863, Bd. XXI, p. 128; Vergleich, Untersuchungen uber Zusammensetzung des Holzkorpers, ibid., p. 396. Ueber die Grosse der Holzzellen in d. gemeinen Kiefer. Pringsheim's Jahrb. f. wissensch. Bot. 1872, Bd. VIII,p. 401. Anat. d. gem. Keifer, ibid. 1873, Bd. IX, p. 50. Compare further Hammerle, Zur. Organisation von Acer Pseudoplatanus. Bibl. Bot. Nr. 50, 1900, and the literature quoted therein.

size of the cell is demonstrable, an examination into the size development of cells for phenomona of arrestment will not be purposeless.

Amelung ascertained that "in the case of parts of plants morphologically equal, the medium cell-sizes remain the same in spite of extraordinary differences in size.[1] The question must still be discussed whether plant organs, dwarfed by the force of abnormal life conditions, lack of water, insufficient nutrition, etc. are composed of elements of equal size with normal organs. If it was necessary above to emphasize the fact that abnormally small organisms or organs are produced exclusively or predominantly by reduction of the cell number, it should now be added, that reduction of the cell size in all cases which are to be designated as arrested developments, in which, therefore no compensation takes place through increase of the cell-number, must lead necessarily to the formation of abnormally small, slender organs. In many cases, moreover, reduction of the cell number is combined with a decrease in cell-volumne. We will therefore have to return repeatedly to the examples given above.

To be sure, dwarf-forms, ataining only a fifth or a
tenth of the normal size, as stated above, do not consist
of cells proportionately decreased in size; yet an evident
reduction of the volumne may be verified, at least in cer-
29 tain kinds of cells. It is interesting that many kinds are
somewhat more susceptible than others and many easily re-
main below the normal size development, while others, even
in highly dwarfed specimens, retain their normal size. Those
tracheal tubes, in which a reduction in diameter may be
constantly recognized, belong to the first class. (Compare
fig. 6). The epidermal cells of leaf blades generally
retain their normal volumne, while the cells of the meso-
phyll are greatly reduced.[2]

Influences, other than those which call forth the "dwarfing" of whole plants, also arrest very appreciably the growth of the mesophyll cells. First of all, a comparison of sun and shade leaves proves this: in the latter not only the mesophyll cells are often greatly shortened, but even the epidermal cells may be very small, for instance, in Ficus stipulata, (compare fig. 8a and b.) The same reduction in cell size may be verified in those varieties with pale green leaves, which Griffon (loc. cit.)

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1. Ueber mittlere Zellengrossen. Flora, 1893, Bd. LXXVII, p. 176. Compare also Schnegg, Beitr. zur Kenntnis der Gattung Gunnera, Ibid., 1902, Bd. XC, p. 161

2. Compare especially Gauchery, loc. cit. As exceptions are mentioned the dwarf leaves of Polygonum Fagopyrum the epidermal cells of which are perceptibly smaller than thosee of normally grown specimens. Compare further H. Moller, loc. cit. Sorauer, Einfluss d. Luftfeuchtigkeit. Bot. Zeitg., 1878, Bd. XXXVI, p. 1.

investigated in variegated plants, in specimens injured by parasites, etc.[1] Finally, cells which are considerably smaller than normal ones may be grown in such a way experimentally that an increase in cell volume is mechanically prevented by putting the young parts of the plant in plaster casts. If the normal process of cell division takes place at the same time, abnormally small cells are produced.[2]

Abnormally narrow tracheal tubes are found not only in the fibro-vascular bundles of dwarf specimens, but also in poorly nourished individuals[3], in etiolated plants, and in individuals infected by fungi or arrested in their development by gall-producing animals.

The products of the cambium also are variously arrested in size, develop ; by diverse factors. Very strong pressure may arrest the normal development of wood cells.[4] In the same way small-celled wood results from disturbances in nutrition. Hartig has proved repeatedly in pines, that the tracheids are smaller in weakly grown specimens than in those normally developed. The
30 lumen width of tracheal tubes in secondary xylem, especially is also easily changed by all possible injurious influences.[5] Among others, Wiedersheim's interesting experiments give much information as to the effect on growth in length of xylem elements.[6].

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1. Timpe, Beitrag zur Kenntnis der Panachierung. Dissertation Göttingen, 1900; Leist, Ueber den Einfluss des alpinen Standorts auf die Ausbildung d. Laubbl. Mitteil. Naturf. Ges. Bern, 1889. Klebahn, Ueber eine Krankh. Veränderung d. Anemone nemorosa etc. Ber. d. D. bot. Gesselsch. 1897, Bd. XV, p. 257.

2. Compare the experiments of Hottes, Ueber den Einfl. von Druckwirkungen auf die Wurzel von Vicia Faba. Dissertation Bonn, 1901.

3. Compare for example, Pethrbridge, Beitr. z. Kenntn. d. Einwirkung der anorganischen Salze auf die Entwickelung und den Bau d. Pfl. Dissertation Göttingen 1899; further bibliographical references therein.

4. Krabbe, Ueber d. Wachstum d. Verdickungsringes u.d. jungen Holzzellen. Abhandl. Akad. Wiss., Berlin 1884, p. 21.

5. Die Verschiedenheiten in der Qualität und un anat. Bau des Fichtenholzes. Forstl.- Naturwiss. Zeitschr., 1892, Bd. 1, p. 209. Wachstumsunters. an Fichten, ibid. 1896, Bd. V, p. 1. Further examples are described by H. v. Mohl (Einige anat. u. physiol. Bemerk. über d. Holz der Baumwurzeln, Bot. Zeitg., 1862, Bd. XX, p. 269: Wieler, Ueber, Bezieh. zw. d. sekund. Dickenwachstum u. d. Ernährungsverhältnissen der Bäume. Tharander forstl. Jahrb. 1892, Bd. XLII, p. 72; Holzbildung auf Kosten d. Reserve-materials der Pflanzen, ibid. Bd. XLVII, p. 172.

6. Ueber d. Einfl. d. Belastung auf die Ausbildung von Holz. und Bastkoper bei Traurbaumen. Pringsheim's Jahrb. f. wiss Bot., 1902, Bd. XXXVII, p 41. Compare also what is stated later for "Rotholz" (Chapter V. A.)

This author ascertained in different woody plants that wood cells could not attain their normal length under the influence of artificial mechanical strain. To be sure, the differences are not very great, in *Fagus silvatica* var. *pendula*, the wood cells of normal branches, for example, bear to weighted ones, a proportion of 33.224 to 29.525, etc.

To return finally to the statements made at the beginning of this section,- it can be proved forthwith that most of the examples of reduction in cell-size given here also furnish examples of the second of the two modes of growth described above. As examples of the first named mode of those given here only the phenomena observed by Klebs in Euastrum come under our consideration,- as well as the case of the plant which had been put into a plaster cast, and which was studied by Hottes.

C. DIFFERENTIATION OF THE CELLS AND TISSUES

An organ attains its specific character through distinct processes of differentiation enacted in its cells rather than by the number and volume of the cells composing it. The cells attain a characteristic form by definitely regulated or localized growth. Further, the histology and physiology of the cell is determined by the formation of living or lifeless cell contents, by thickening of the cell walls, and by modification of its chemical composition. In most cases, the formation of the cells of an organ differs according to their position in it, so that finally the matured organ is composed of elements of very different kinds.

In the study of arrested developments, those cases come first under consideration in which the formative process of individual cells stops prematurely, so far as form, wall, or contents are concerned; secondly those in which the cells of a tissue or an organ, varying in the same sense from the normal procedure, are developed and produce a homogenous tissue instead of well differentiated layers.

1. FORMATION OF THE CELL

Both of the essential elements of the cell,- cytoplasm
31 and nucleus,- are excluded here from our discussion. As yet, only very little has been definitely ascertained concerning the structural peculiarities of cytoplasm and only in isolated cases have we been half way instructed ontogenetically about the production of definite structural differences. Conditions, so far as the nucleus is concerned, are more favorable. In some ciliates (Oxytrichides), in the formation of nuclei, with two or more parts, or even rosette-like, and in the distinctive formation of macro- and micro-nuclei, we may see complicated processes just as in the phenomena visible in karyokinesis, the production of which may doubtless be arrested or completely suppressed by more or less violent experimental interference. As is well-known, it has been possible repeatedly to cause the production of the more simple amitotic stages of cell-division.

instead of complicated karyokinetic ones.[1] Since cytological problems lie outside our subject, we return, with this one reference, to the treatment of the grosser anatomical structures.

FORM OF THE CELL

The more highly organized a cell form may be under normal conditions, the more susceptible it is to the action of factors which arrest development.

In higher plants, we usually find only very simple cell forms in individuals normally matured. However, "protective palisade cells" may be cited as examples of the opposite. In fact in gymosperms as in angiosperms it may be proved, that under abnormal life-conditions, the "protective palisade" cells may be replaced by simple cell forms. The needles in Pinus austriaca, developed in Bonnier's[2] experiments under consant illumination,- we will return later to this series of experiments,- contained simple polyhedric parenchyma elements as shown in figure 9, instead of the normal protective palisade cells. Klebahn (loc. cit.) observed the same replacement by simpler forms in leaves of the anemone, after fungus infection.

The arresting action of unfavorable life conditions upon the development of the cell form may be pointed out much more emphatically in the unicellular, highly organized Siphoneae. The Codiaceae are easy to investigate and are especially instructive. In normal specimens of <u>Udotea Desfontainii</u> the leaf-like part of the thallus is composed of elongated sacs, arranged parallel and extending lengthwise, from which spring numerous, diversely ramified side-branches with a limited period of growth. The later in turnn are also extensively branched and repeatedly lobated and dove-tail themselves together by means of their short ramifications,[3] thereby giving the thallus the necessary firm
32 consistency. Under artificial cultivation, extending over several months, the appearance is completely changed. The above mentioned papallel sacs show an abundant and undiminished growth activity which is often indeed increased, branching abundantly but not forming any more "stunted shoots", The firm connection between the single sacs is thus lacking; the thallus totally loses its characteristic form, the isolated sacs form a loose green reticulum over the neighboring ones;- the formal and functional difference between the single parts of the cell is lost entirely. <u>Codium tomentosum</u>

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1. Compare Gerassimow, Die kernlosen Zellen d. Conjugaten Bull. Soc. Imp. Natur. Moscou 1892; Nathansohn,Physiol. Untersuch. ub. amitotische Kernteilung. Pringsheim's Jahrb.1900. Bd. XXXV,p. 48;Hacker,Mitosen im Gefolge amitosenahnlicher Kernteilungen. Anat. Anz., 1900, Bd. XVII, p. 9.
2. Bonnier. Infl. de la lumiere electr. continue s. la forme et la struct. d. pl. Rev. gen. de Bot.,1895, T.VII,p.241
3. Illustration in Küster Anat. und Biol. d. adriat. Codiaceen. Flora, 1898, Bd. LXXXV, p. 181.

behaves in the same way. The outer layer of its normal thallus is composed of "palisade tubes", swollen to a club shape, and arranged perpendicular to the surface. On their tips arise the slender unbranched "trichome tubes" which are sharply cut off from them. All these differences are lost during longer cultivation. The trichome tubes become similar to the others, if still at all recognizable, as such, they branch extensively, etc. It is not known as yet whether in these and similar cases the arrested developments may be traced back to scarcity of light, insufficient oxygen supply, or to other factors. Finally the phenomena of arrestment exhibited by Struvea should be considered. They furnish indeed nothing essentially new, but may find mention here because of their biological interest. According to Weber van Bosse [1], Struvea delicatula lives at times in symbiosis with a fungus (Halichondria) but then only develops filaments, resembling Vaucheria, instead of the characteristic extensively branched shoots, just as do the Udotea and Codium specimens in our cultures. The author compares the form of the alga, simplified by symbiosis, to Spongocladia vaucheriaeformis. Undoubtedly, her observations may be placed in line with those quoted above.

Also in the case of the more simply formed Siphonaceae, the distinct formation of different cell parts is omitted under certain conditions, for example in Bryopsis.
33 In Vaucheria the vegetative parts of the filaments are known to be all alike. Only those parts of the cell serving for propagation are differently constructed. That even this difference in form may be lost, is proved by the oogonia which develop vegetatively.[2]

In the case of the Diatomeae and Peridineae also, in which highly organized cell-forms are abundant, analogous "simplifications" must be found if one looks for them. Rattray described abnormal forms for Aulacodiscus, in which the characteristic protuberances were lacking.[3] Of the unicellular Chlorophyceae, Scendesmus acutus, for example, comes under our consideration, which with an excess of organic food, may lose its tips,[4] etc.

CELL MEMBRANE

Arrested development of the cell membrane is expressed for the most part by the partial or entire cessation of its secondary growth in thickness. The cells of the epidermis, the ducts, the sclerenchyma and collenchyma cells then show only moderately thickened walls, or the formation of

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1. Etudes s. des. algues de l'archipel malaisien I. Ann Jard. Bot. Buitenzorg, 1890, Vol. VIII, p. 79.
2. Klebs, Beding. d. Fortpfl. bei einigen Algen und Pilzen. Jena k896, p. 102.
3. Notes on some abnormal forms of Aulacodiscus Ehrb. J. of Bot., 1888, Vol. XXVI, p. 97.
4. Beijerinck, Kulturversuche mit Zoochlorellen, Lichenengonidien u. s. w. Botan. Zeitg., 1890, Bd. XLVIII, p. 724.

the sclerenchyma and collenchyma may even be entirely suppressed.

In most cases, hypoplasia is caused by disturbances in nutrition,- it being immaterial whether shade plants and shade leaves are concerned, plants cultivated under water or in places saturated with vapor, whose transpiration current is thus insufficient for providing them with the necessary food stuffs, also etiolated specimens, or even when the disturbance is caused by infection with parasitic fungi.[1] In all cases, as far as the membrance is concerned the same symptoms are involved. At the same time, in all plants having insufficient transpiration currents, we may prove that there is only a weak development of the cuticle of the epidermal cells. Weakly developed cell-membranes are frequently found in dwarfed specimens, in which the formation of the mechanically effective tissue is often entirely suppressed.[2] When diatoms under unfavorable life conditions show a more weakly developed shell structure than under normal conditions, it may be traced back to similar arrestment of the growth in thickness. According to
34 Heribaud [3], the striation of the shells of Gomphoema, Navicula, Stauroneis, and Synedra, is only slightly pronounced when the cultures are kept in weak light. According to Karsten [4], the formation of the little silicious rods in Sceletonema costatum is suppressed when the organisms are left absolutely undisturbed on the bottom of the culture dish. In the first case, the arrestment of the cell-membrane development may be traced back to the decreased assimilatory activity of the cells; in Karsten's experiment the dormant cells will also have been placed under more unfavorable nutritive and respiratory conditions than those cells which, in uninterrupted passive motion, are carried continuously to layers of water containing food-stuffs, and rich in oxygen.

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1. Compare the above mentioned literature on shade leaves, as well as the articles quoted in Chapter IV, 2. Further, Wakker, Untersuchungen über den Einfluss parasitischer Pilze auf ihre Nahrpfl., Pringsheim's Jahrb. f. wiss Bot., 1892, Bd. XXIV, p. 499. Tubeuf, Pflanzenkrankh. durch kryptogame Parasiten verursacht. Berlin 1895, p. 53, ff. Kny, Eine Abnormität in der Abgrenzung der Jahresringe. Sitz.-Ber. Naturg.- Fr. Berlin, 1890, p. 138 (Thin walled autumn wood). It is very remarkable that in badly nourished specimens the cells in the central cylinder of the roots have abnormally thick walls. (Observations on water cultures by Pethybridge loc. cit.). (Compare Chapter III).

2. Compare especially Gauchery, loc. cit.

3. De l'infl. de la lumiere et de l'altitude sur la striation des valves des Diatomees. C. R. Acad. Sc. Paris, 1894, T. CXVIII, p. 82.

4. Die Formveränderung v. Sceletonema costatum (Grev) Grun und ihre Abhängigkeit von äusseren Faktoren. Wissensch. Meeresuntersuch., 1898, Bd. III, p. 13.

Secondly, chemical changes, which the cell wall in many cases, undergoes in the course of its development, especially in a process of lignification, must be considered. While the growth in thickness of the cell wall may be arrested in different plants, and by very different kinds of disturbing influences, the cases are rare in which thickened cell walls, like those of the sclerenchyma, the ducts, etc. are excluded from lignification. Examples are furnished by the Crataegus branches infected with Roestelia, of which the medullary parenchyma remains unlignified (Wakker loc. cit.), the Raphanus shoots attacked by Cystopus, whose ducts remain unlignified, etc.[1] It is remarkable that even under the life conditions, which are furnished our fruit trees under cultivation, the lignifying process may be omitted. Perhaps abundant water supply and excessive nutrition are the decisive factors. Sorauer[2] found partially unlignified pith in the fruit spurs.

Finally, the phenomena of reabsorption must be considered, which under normal conditions, occur in the membranes of many cells and lead to the building of the so-called cell fusions, for instance in the sieve tubes. Under nonmal conditions this reabsorption can be omitted, for example, only tracheids may be developed instead of ducts. Since, under the action of unfavorable life conditions. the width of the lumen of the ducts decreases greatly, it is not always easy to give information concerning the occurrence or the omission of this fusion. Wakker found that reabsorption was omitted in different plants which were infected with fungi (Vaccinium with Exobasidium, Crataegus with Roestelia, Rhamnus with Aecidium). Doubtless, in etiolated leaves and stems and in individuals which have matured with arrested transpiration, the same arrestment may be demonstrated in the formation of the elements which convey water.

Finally under the influence of arresting factors, the formation of cross walls may remain so incomplete, that instead of separate spaces, chambers may arise communicating with one another, or in the end, the formation of the cross walls is entirely omitted. If the cells continue their growth simultaneously, abnormally large cells are produced, and if their nuclei also divide at the same time they result
(35) in multinucleated cells of abnormal capacity. For the present, we will be content with a brief reference to arrested developments of this kind. On account of the external conformity existing between cells of abnormal size produced by arrestment of the membrane formation, and those of abnormal size developed by abnormal growth (hypertrophy) we will postpone their closer discussion to the fourth chapter.

In what way arresting factors influence the development of cross walls has been ascertained as yet only

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[1] Peglion, Studio anat. di als. impertrofie indotte dal Cystopus candidus in als. org. di Raphanus Raphanistrum. Riv. pat. veg. 1892, Vol. I, p. 265.

[2] Nachweis der Verweichlichung der Zweige unserer Obstbäume durch die Kultur. Zeitschr. f. Pflanzenkrankh., 1892, Bd. II, p. 66, 143.

for a few cases. It is known that newely produced cross walls are formed from the system of kinopessmatons. "spindle fibres", which become visible during karyokinesis, or remain independent of the nuclear division figure. After it has been proved that karyokinesis may be replaced by simpler amitotic stages of cell division, by means of various kinds of experimental interference, we will have to investigate more closely in what way normal amitotic division of the body influences the mode of formation of cross walls.

In Oedogonium, whose cross wall formation is known to be initiated by the deposition of a cellulose ring, a simplified mode of wall formation without the celluose ring may be observed as the result of abundant sugar nutrition.[1]

CELL CONTENTS

Of the special contents of the plant cells which come under our consideration, the chromatophores and especially the chloroplasts are the most important, not only on account of their wide distribution in the plant kingdom and their important physiological significance, but also on account of their sensitiveness to various external factors, by which their development is easily and often arrested.

The development of the chloroplasts can be arrested in many ways,- the number of chlorophyll grains which are united in one cell remains below the normal, or the individual chlorophyll grains do not attain their normal character, remaining small, or free from chlorophyll, or they end their existence as chlorophyll grains, instead of developing into yellow or red chromatophores.

The number of chlorophyll grains remains below normal in the cells of many variegated leaves, in many varieties with pale green leaves,[2] and in plants cultivated in places with atmosphere saturated with vapor. Under the same conditions, the size of the individual grains also is often abnormally small. I do not doubt that under the influence of certain "arresting" factors, even the form of those individual chromatophores can undergo a "simplification", which, as is well known in the gase of many green algae, diatoms and brown and red algae, are remarkable for their complex characteristic organization.

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Those cases demand especial attention in which the formation of the characteristic green coloring matter, the chlorophyll, in the chromatophores, is abnormally omitted. As is well known, the formation of the chlorophyll takes place only within certain temperature limits. It presupposes, further, with some exceptions, the action of light,

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1. Klebs, Bedingungen der Fortpfl. Bei Algen und Pilzen Jena, 1896, p. 288.
2. Compare Griffin loc. cit.

the presence of iron and of certain organic food materials.[1] Hence it follows that under differently combined, abnormal life conditions, the formation of the green coloring matter may be suppressed. It is known that, in the spring, without experimental interference, temperature can influence bulbous growths, grain seedlings, etc., and that these at a low temperature develop yellowish leaves.[2] The minimum temperature for chlorophyll formation in the "variegated" cabbage variety, Brassica oleracea acephala, studied by Molisch[3] is much higher than in the above case. In cold frames, at a temperature of 4 to 7 degrees C. in winter, the plants developed green and white dappled leaves, or leaves completely free from chlorophyll, which, however, became green later if the plants were brought into a temperature of from 12 to 15 degrees C. The leaves newly formed in the warm chamber were always perfectly green. The fact that, under the culture in the cold frame, the leaf tissue near the veins remained predominantly free from chlorophyll, while the other parts of the lamina developed the coloring matter in a normal manner, is worth consideration.[4]

The influence of nutrition may not be ascertained so easily by experiment, since the chemical compounds important for the formation of chlorophyll are produced by the activity of the cells themselves. But the observations should indeed be considered here, regarding the close connection which appears to exist between the leaf variegation of "variegated" plants, and the place in which they grow. According to Ernst[5], a variegated specimen of Solanum aligerum, transplanted into garden soil, became monochromatic.

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1. On the necessity of the latter, compare Palladin. Ergrünen and Wachstum der etiolerten Blätter. Ber, der Deutsch. bot. Ges., 1891, Bd. IX, p. 429.

2. Compare Sachs, Ueber den Einfluss der Temperatur auf das Ergrünen der Blätter. Flora, 1864, Bd. XLVII, p. 497. Wiesner, Entstehung des Chlorophylls, 1877, p. 95. Ritzame Bos, Ergrünungsmangel infolge zu niederer Frühlingstemperatur. Xeitschr. f. Pflanzenkrankh., 1892, Bd. II, p. 136.

3. Ueb. die Panachüre des Kohles. Ber d. D. bot. Ges. 1901, Bd. XIX, p. 32.

4. Timpe (loc. cit . p. 7) reports on a specimen of Ulmus scabra var. viminalis in the Botanical Garden in Göttingen, whose spring shoots bore leaves speckled with yellow, which retained their variation until autumn, while the mid-summer shoots developed pure green leaves. It may be possible that here also an effect of the lower spring temperature is present. Also, as is well known, in bulbous growths, forced in spring, the pale color remains constant in spite of a subsequent increase of temperature.

5. Botan. Miscellaneen. Bot. Zeitg., 1876, Bd. XXXIV. p. 33.

Boucha[1] made similar statements concerning Plectogyne, Phalaris, Zea, Kerria, etc. Fortunately, we have had no thoro and reliable test of the question as to the influence exercised by the quality of the soil, the supply of water, and of light on plants tending toward variegation. The question also, whether the pecularity of the white leaved condition may be carried over to normally colored specimens by scions or by inoculation with sap, has not yet been suffi-
(36) ciently explained. The supposition of a "contagium vivium fluidum" which Beijerinck [2] had suggested, appears but little suited for solving the problem. That unknown individual pecularities play a part in the appearance of white leaved plants, is made probable by the often observed seedlings free from chlorophyll which appear here and there among those which have become green normally.

The effect of <u>deficiency</u> of <u>light</u> and <u>iron</u> is sufficiently well known. In the dark, or without iron, pale plants are produced which are capable of developing only a yellowish colloring matter, instead of the normal green pigment. According to Kohl's recent investigations,[3] the yellow pigment is to be designated carotin. The deficiency of normal pigment in specimens cultivated in the absence of iron, is termed chlorosis or icturus, with plants grown in darkness, it is known as etiolation. In plants which grow in a substratum containing iron, the symptoms of chlorosis may also become apparent if the cells of the plant or definite parts of them are incapable of taking up sufficient amounts of iron. The chlorosis found in vines appears to be of this kind.

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1. Sitzungsber. Ges. Naturf. Freunde Berlin, 1870, p. 40 and 1871, p. 19, 66. Compare here also Lindemuth. Vegetative Bastarderzeugung durch Impfung. Landwirtsch. Jahrb., 1878, Bd. VII, p. 887.

2. Ueber ein contagium vivum fluidum als Ursache der Fleckenkrankh. der Tabaksblätter. Centrabl. f. Bakteriol etc., 1899, 2. Abth. Bd. V, p. 27. Further, the attempt at explantation made by Woods should be mentioned, (The destruction of chlorophyll by oxydizing enzymes. Ibid., p. 745), which calls attention to the richness of variegated leaves in oxydizing enzymes and to the action of these in destroying chlorophyll. The same author published ")bservations on the Mosaid disease of tobacco" (United States Department of Agriculture, B. P. D. Bull, No., 18, 1902). The oxydizing enzymes produced after injury, as well as under the influence of poisons after parasitic infection will have great significance undoubtedly for the pathology of plant cells and tissues. (Compare besides Janowski in Ztschr. f. Pfl.- Krankh. 1902, Bd. XII, p. 202.)

3. Untersuchungen Uber das Carotin und seine phys. Bedeutung in der Pfl. Leipzig. 1902.

Above all others, the seedlings of many gymnosperms and also various algae are to be counted as exceptions to the rule, so far as the need of light is concerned. They become green even in the dark, if the food materials of the endosperm are at their disposal , ie. if organic food is furnished them from without.[1] Well worth noticing is the fact, that the formation of chlorophyll can be suppressed, at least for lower organisms, buy an over-abundant supply of organic food. Zumstein [2], obtained in this way colorless Euglena (E. gracilis) in which the green color was restored by the use of organic substances. Karsten[3] found analogies in diatoms.

38 All organs, not turning green normally, but for some reason, remaining colorless or yellow, contain chromatophores which are yellowish pigmented or completely colorless. Their number per cell often remains below the normal, their size usually is sub-normal also; often chromatophores being demonstrable only in the form of tiny grains. In many kinds of variegated leaves, they appear to be entirely lacking in the white parts, as, for instance, according to Winkler[4] in Pandamus Veitchi.

Finally those arrested developments should be considered, in which normal chlorophyll grains are indeed, developed but are "hindered" from transforming into yellow or red chromatophores. A good example of this is given by the green flecked lemons, where the ripening processes have been checked on the spots infested by Aspidiotus narii.[5] Even autumnal coloration can be prevented in places by external factors

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1. Literature citations Artari, Zur Ernahrungsphys. d. grunen Algen. Bericht d. D. Bot. Ges., 1901, Bd. XIX, p.7. Compare also Matruchot and Molliard. Variations de structure sous l'infl. du milieu nutritif. Rev. Gen. Bot. 1902,T.XIV,113.

2. Z. Morph. u. Phys. der Euglena Gracilis. Pringsheim's Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 149. Compare Beijerinck, Kulturversuche mit Zoochlorellen etc. Bot. Ztg.1890, Bd. XLVIII, p. 724 (Beobacht. an Scendesmus); Krüger, Ueb. einige aus Saftflüssen reingezüchete Algen. Zopfs Beitr., 1894, Bd. IV, Kurze Charakteristik einiger neid. Organismen im Saftflusse d. Laubbäume. Hedwigia, 1894, Bd. XXXIII,p.241. Matruchot and Molliard, Variations de struct. d'une Algue verte etc., loc. cit.

3. Ueb. farblose Diatomeen. Flora, 1901 (Erganzungsband) Bd. LXXXIX, p. 404.

4.Untersuch. über d. Stärkebildung in d. verschiedenartigen Chromatophoren. Pringsheim's Jahrb. f. wiss. Bot.1898, Bd. XXXII, p. 525. Compare also Frank, Krankh. d. Pfl., 2, Aufl. Bd. I, p. 225, and other places. Zimmermann, Morph. u. Phys. d. Pflanzenzelle, 1893. p. 31, 53; Timpe. loc. cit., Pantanelli, Studi sull' albinismo vel regno vegetale. Malpighia, 1902, Vol. XV, p. 363.

4. Kocks, K. Beitr. z. Einwirkung d. Schildläuse auf das Pflanzengewebe. Jahrb. Hamburg.wiss.Anat.1900, Bd.XVII,3.Beiheft

5. Einfl. d. Lichtes auf d. herbstl. Verfärbung d. Laubes Sitzungsber. Niederrhein. Ges. Natur - u. Heilkunde-Bonn, 1891, p. 80.

Noll observed in Ampelopsis, etc,[1] that leaves partly covered by other leaves did not turn red. At times one can also perceive in leaves infected by fungi, that certain parts remain green for a noticeablly long time.

In connection with chromatophores, a few other brief remarks on the red pigment of plants (anthocyanin) are appropos. Its formation also is connected with definite conditions. In the study of these we meet again with the factors which are concerned in the formation of chlorophyll; first of all, light. The dependence of the anthocyanin formation upon the action of light differs from that of the chlorophyll formation in that only in the case of certain plants and organs is light indespensible for the development of the red coloring matter. Many rhizomes, roots, bulbs, and tubers which, under normal conditions, remain continuously without light, are richly provided with anthocyanin. On the otherhand, there are organs which develop the red coloring matter only upon exposure to light; for instance, seedlings of Polygonum fagopyrum, which Batalin[2] investigated carefully. The fact has long been known to breeders and to those interested in plants, that the formation of pigment is suppressed in red leaved ornamental plants cultivated in the shade. According to Pynaert, the dependence upon light is especially noticeable in Alternanthera atropurpurpa and Coleus.[3] The blossoms of many plants also need
39 the action of light for the development of their red and blue pigments; other plants, however, open normally-colored blossoms in the dark, or blossoms that remain only a little below the normal in the intensity of their coloring. In Orchis ustulata , only the hood loses its color.[4] Fruits, as well as blossoms, behave dissimalarly in the formation of pigment under abnormal conditions of life. The fact that apricots, apples, pears, etc. only redden on the side exposed to the sun, has been cited often since Senebier. On the other hand, Laurent[5] has proved that vines with blue

1. Einfl. d. Lichtes auf. d. herbstl. Verfarbund d. Luabes. Sitzungsber. Niederrhein. Ges. Natur - u. Heilkunde Bonn, 1891, p. 80.

2. Die Einwirkung des Lichtes auf die Bildung d. roten Pigm. Acta Horti Petrop., 1879, T. VI.

3. De l'infl. de la lumiere sur la veget. de pl. cultivees en serre. Bull. Congr. Intern. de Bot. et d'Hortic.1884, p. 229. Therein also further examples (Dracaena, Pandanus Veitchi, Saxifraga and others.) The leaves of the red beet develop red coloring matter even in the dark(predominantly on the veining.

4. Compare the notes by Askenasy, Ueber den Einfluss des Lichtes auf die Farbe der Blüte. Bot. Zeitung, 1876,Bd. XXXIV, p. 1. also Benlaygue, Infl. de l'obscurite s. l. devel. d. fleurs. C. R. Acad. Sc. Paris 1901,T.CXXXII, p. 720.

5. Infl. de la radiation s. la coloration des raisins. C. R. Soc. Roy. Bot. Belgique. 1890, T. XXIX, 2. p. 71.

fruits are not dependent on the action of a direct supply of light for the formation of their pigment. In all cases in which an interdependence between exposure to light and formation of pigment may be recognized, we may venture to assume that a specific action of light does not lie at the root of the matter, but that nutritive conditions, altered by the influence of the light represent the decisive factors. Askenay (loc. cit.) observed that shoots of Antirrhinum majus and Digitalis purpurpa, from which the leaves had been removed, developed white blossoms, clearly the result of a disturbance in nutrition due to the loss of the leaves. Laurent (loc cit.) obtained the same results by shading the leaves, while letting the blossoms develop in the light. Unfortunately, he did not name the plants with which he experimented. In the case of Syringa the inflorescences, below which Laurent had girdled the branches, developed only pale blossoms, the grapes from blue stock were incompletely colored if the food supply was cut off by girdling. Coloration was entirely absent if the grapes of girdled shoots were also kept at the same time in the dark. Accordingly, it is very probable that blossoms which, under normal nutritive conditions, can develop their pigment only by exposure to light, can become red or blue even in the dark, if in some artificial way the necessary food stuff can be supplied them in sufficient quantities. Doubtless, it will also be possible to suppress the formation of red pigment in blossoms by unfavorable conditions of transpiration.

Finally the influence of climatic pecularities on the formation of pigment may also be explained by disturbances in nourishment. The reports that Petunia and Brachycome in India[1] as well as Carduus nutans in the neighborhood of the sulphur baths of Pjatigorek (Russia)[2] deserve consideration and indeed, confirmation. For the present, the factors are still unknown which cause the appearance of so-called albinos in different plants,- individuals with white bloosoms or fruits, instead of those normally colored red. The fact that many homogenous bacteria, under certain
(40) cultural conditions, temporarily lose the ability of producing coloring matter, for instance, Micrococous prodigiosus at a high temperature (40 Degrees C.) may be mentioned in passing. With the bacteria whose formation of pigment may be suppressed, the coloring matter is not found in the cells themselves, but is excreted by them into the surrounding medium.

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1. Gard. Chron., 1881, 1, p. 627.

2. Riesenkampf, Bemerkungen über einige in verschiedenen Gegenden des russischen Reiches vorkommende Anomalien in der Form and Barbe der Gewachse. Bull. Soc. Imp. Natur. Moscou, 1882, p. 85.

We can dispose briefly of the cell inclusions which, in additions to the chromatophores, come under our consideration. Particularly important are the crystals of calcium oxalate, the formation and distribution of which is, to a high degree, dependent on external factors. A. F. W. Schimper, Kohl, Wehner, and others[1] have already furnished contributions to the knowledge of the conditions under which the normal formation of the crystals takes place, Their results, however, are not without contradictions and a thorough comprehensible treatment of the question is still wanting. It may only be said with certainty that lowered transpiration decreases the number of crystals; shade leaves contain fewer crystals than do sun leaves and specimens cultivated in moist air, or without light, are also poor in crystals, as likewise are parts of variegated leaves free from chlorophyll. According to Rauwenhoff[2], etiolated specimens of Polygonum cuspidatum entirely lack crystalls. More investigations of this would be desirable. Vandevelde[3] proved further , that leaves bearing galls are especially poor in crystals. Future investigators will have to notice whether abnormal life conditions can also influence the form of the individual crystals and possibly prevent the develop-

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1. Schimper, A. F. W. Ueber Kalkoxalatbildung in den Blättern, Bot. Zeitg., 1888, Bd. XLVI, p. 65. Kohl, Anat,-phys. Untersuchungen der Kalksalze und Riesselsalze in der Pfl., Marburg, 1889, p. 50, and elsewhere. Wehmer, Die Oxalatabscheidung im Verlauf der Sprossentwicklung u. s. w. Bot. Zeitg. 1891, Bd. XLIX, p. 149. Zur Frage nach dem Fehlem oxals. Salze. Landwirtsch. Versuchsstat., 1892, Bd. XL, p. 109. Among other literature may be mentioned, Monteverde, Uber den Einfluss des Lichtes auf die Bildung des oxals. Kalkes in der Pfl. (Russian). Arb. Petersb. Naturf. Ges. Bd. XVIII, p. 46. Cuboni, App s. anat. e fisiol. d. foglie d. vite. Riv. Enol. e Viticolt., Serie II, Vol. II (compare Bot. Cbl., 1884, Bd. XVII, p. 332). Dufour, Infl. de la lumiere s. la forme et la struct. d. feuilles. Ann. Sc. Nat. Bot. VII, serie, T. V. 1889, p. 311. Buscalomni. Studii sui cristalli di ossalato di calcio. Malpighia, 1896, Vol. IX, p. 469.

2. S. l. causes et l. formes anormales d. pl. qui. croissent d. l'obscurite. Ann. Sc. Nat. Bot., VI. Serie, T. V. 1877, p. 267.

3. Bijdr. tot de phys. d. gallen; het aschgehalte d. angetocte bladern, Bot. Jaarb. Dodonea, 1896, Bd. VIII, p. 102.

ment of regular individual forms. It is but natural that the formation of the calcium-oxalate crystals is greatly retarded or entirely absent in the culture of seedlings in media free from calcium. Cysoliths behave like crystals, their normal development being conditioned by the calcium supply. If this is lacking, according to Charyre[1] only the stem of the cystolith will be deposited, the formation of the cellulose head being omitted. Cystoliths are scantily formed in leaves sufficiently exposed to the light.[2] Hence, as in the cases reported above, a lowering of the transpir-
(41) ation seems to be determinative; at least I have obtained rudimentary cystoliths in leaves of Ficus elastica, if transpiration was arrested, even with a continuous exposure to light. Etiolated leaves of Acanthaceae form normal cystoliths, while, under the same conditions, in Moraceae and Urticaceae these remain rudimentary. The calcium incrustations are arrested by lack of light. The hairs of the Boragineae also remain poor in calcium in etiolated specimens, (according to Chareyre.) Melnikoff reported cystoliths free from calcium.[3]

2. DIFFERENTIATION OF THE TISSUE

An arrestment of tissue differentiation occurs in all those cases in which the elements of certain cell complexes develop in the same way as contrasted with the fact that under normal conditions, certain individual cells or cell groups would be formed differently from adjacent ones. Hypoplasia is thus shown, in that a homogenous tissue is produced, where under normal conditions we find one composed of well-differentiated layers and groups. It is evident that this kind of hypoplasia cannot find expression in all organisms. We must at once exclude the unicellular organisms, which do not live in colonies, and the multicellular ones composed only of similar cells. As is well known, however, in most multicellular plants,- even in the algae and fungi, an evident tissue differentiation is recognizable.

Before we pass to these, a few words are necessary concerning unicellular organisms. Only those come under our consideration which are united into colonies with easily distinguishable components, as, for instance, many of the plankton diatoms which form chains, the end member of each chain often being differentiated from the others. Colonies of Scendesmus caudatus behave similarly; their end cells are

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1. S. L'origine et la formation trichomatique de quelques cystoliths. C. R. Acad. Sc. Paris, 1883, T. XCIII, p. 1073. Sur la form. d. cystol. et leur resorption. Ibid., p. 1594. Nouv. Rech. s. l. cystol. Rev. d. Sc. Nat., Montpellier, III, Serie. T. III, p. 523.

2. Ficus elastica according to Kohl, loc. cit. p. 39

3. Untersuch. üb. d. Vorkommen d. $CaCO_3$ in Pfl. Dissertation Bonn, 1877, p. 35. Compare with this also Kohl, loc. cit. p. 141, and the observations of Mollisch on Cystoliths normally free from calcium (Oest. Bot. Zeitschr., 1892, Bd. XXXII, p. 345.)

furnished with long delicate gelatinous horns. As Senn[1] has shown, the formation of the horns is lacking under abnormal life conditions, nutrient solutions, in the usual concentration and rich in oxygen or highly concentrated nutrient solutions without the addition of oxygen, while the gelatine is formed as a uniform coating on all parts of the colony. A similar arrestment in the differentiation of the colonies might also be obtained, under certain conditions in the diatoms just mentioned, or in Pediastrum granulatum, whose lamelliform colony is composed of polygonal cells two-armed at the edge, etc. The same arrestment may be studied further in the colonies of individuals lacking membrane such as those known as plasmodia in the Myxomycetes. When the fruit bodies of Dictyostelium mucoroides are being formed under normal life conditions, a division of labor appears among those individuals which have united themselves into a plasmodium (rather, a pseudoplasmodium) of such a kind, that a part of the Amoeba mass is used for the forma-
(42) tion of a stem, and the rest is transformed into spores.[2] Recently the interesting evidence has been produced by Potts that[3] under certain abnormal conditions this differentiation is omitted, that under water, as well as on concentrated nutritive agar (5.5. per cent. KNO_3) the whole amoeba mass is transformed into spores and that, conversely, in development under a layer of oil, sterile stem cells are formed without exception. Consequently, first one and then the other process of differentiation is eliminated from the course of development of the cell aggregate.

As far as the differentiation of the tissues of the multicellular growths is concerned, it may be said, regardless of their diversity, that there is, in general, no organ whose tissues could not be arrested in their differentiation by factors acting more or less energetically. Thus, as before, we will limite outselves to the treatment here of a few tissue forms.

Observations on the arrestment of tissue differentiation may be made so easily, without troublesome experiments that there exists a real superfluity of reports on this subject. In listing the authors, a choice will therefore suffice, especially as many of these reports give inadequate data.

From the list of thallophytes and cellular cryptogams the Narchantiaceae furnish an instructive example. The structure of the normally developed thallus is well known.
(43) Its elements are at the left in figure 10; an epidermis

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1. Ueber einige koloniesbild. einzellige Algen. Bot. Zeitung, 1899, Bd. LVII, p. 39.

2. Brefeld, Untersuch. aus. d. Gesamtgebiet d. Mykologie, Heft VI, Göbel, Organographie. 1898, p. 21.

3. Zur. Physiologie des Dictyostelium mucoroides. Flora, 1902, Bd. XCI (Ergänsungsbd.) p. 281.

(43) which bears rhizoids; a colorless parenchyma free from interstices, the cells of which have in part slightly rericulated and thickened walls; an assimilatory parenchyma and an upper epidermis, broken through by breathing pores. This complicated structure is almost entirely lost in specimens cultivated in weak light or in rooms saturated with vapor. The assimilatory threads, lying under the epidermis of the upper side, and the thick-walled parenchyma cells disappear entirely; the thallus is composed in all its parts of similarly formed cells; small amounts of chlorophyll may be found in all the layers, in a superficial position somewhat more abundnatly than in a more dedial one. (Compare fig. 10, right.)[1]

Various other interesting examples might still be chosen from the list of Bryophytes, of which I will here name only two. In Bryum argenteum the cells in the UPPER PART OF THE LEAVES dies and fill with air, thereby giving a characteristic silver sheen to the shoots. As Gobel has proved,[2] this differentiation of the leaf is lacking when the moss is cultivated in a damp place ; the cells of the leaf apex remain alive and green. This differentiation, originating through the dying off of certain cell groups, is found also in other moss varieties and may be suppressed in them (Compare Göbel) Leucobryum glaucum retains its structure, even when it is cultivated under water. Oehlmann[3] observed, further a lack of differentiation in the "rudimentary leaves" of Sphagnum which he obtained by cultivating the moss in poor nutritive media and with weak exposure to light. While normal leaves are composed of small green and large colorless cells, both kinds of cells are about equally large in the rudimentary leaves and also arranged essentially different from those in the normal leaf. As a matter of course, entirely similar phenomena of arrestment may appear also in the richly differentiated tissue of many Euthallophyte groups; marine algae furnish favorable material[4], especially those specimens which are

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1. Stahl, loc. cit. Ruge, Beitr. z. Kenntn. d. veg. Org. d. Lebermoose, Flora, 1893, Bd. LXXVII, p. 294. Beauverie, Etude d. modific. morph. et. anat. de thalles de Marchantia et de Lunularia obtenues experimentalement. Soc. Linn. Lyon 1898, T. XLIV p. 57, Gobel. Organographie, 1901, p. 301, etc.

2. Ueb. d. Einfl. dl. Lichtes auf. d. Gestaltung der Kakteen u. and Pfl. Flora, 1896, Bd. LXXXII, p. 1. Further Organographie, p. 368. Compare also Geneau De Lamarliere and Maheu, J. Sur le flore des mousses des cavernes. C. R. Acad. Sc. Paris, 1901, T. CXXII, p. 921.

3. Veget. Fortpfl. d. Sphagnaceen etc. Dissertation Freiburg i. Schw. 1898.

4. Compare for example, Peterson. Note s. l. crampons chez le laminaria saccharina, Bot. Not., Bd. XXI, p. 319.

grown in artificial cultures,- also Hymenomycetes. In mines and other moist localities without light, deformed mushroom have repeatedly been collected, whose tissue differentiation remains sub-normal.[1]

(44) In the vascular plants, we will briefly discuss in order the formation of the epidermis, the mesophyll and the conducting and mechanical tissues.

Epidermis, mesophyll. In cross sections through leaves and stems, one usually finds the epidermis, in so far as the primary dermatogen is still retained, sharply separated from the tissue lying beneath it. Taking no account of differences in size existing, on the one hand, in cells of the epidermis, and the other hand, in those of the mesophyll and the primary bark, the distinguishable content of chlorophyll, the characteristic form of the mesophyll cells, the thickening of the walls of the bark cells, and many others, may still become important, according to the plant species concerned. The difference between the epidermis and the tissue layers lying beneath it, can be eliminated or at least decreased since the inner tissues lose their capacity for characteristic formation, as in the needles of Pinus austriaca, illustriated in figure 9, in which the cells of the hypoderm as well as those of the epidermis have remained thin-walled, or as in many dwarf specimens in which there is lacking a formation of mechanical tissue in the bark.[2] This can also take place if the cells of the epidermis follow the course of development that under normal life conditions falls only to the lot of the more deeply lying layers. Abundant chlorophyll is developed in submerged epidermal cells, for instance, in the leaves of Sagittaria, which are forced to develop below the surface of the water.[3]

If the cells of the epidermis are compared with one another a very different degree of "division of labor" may be recognized in their formative and functional characters; not infrequently, such a division is lost altogether. In many leaves the epidermis of the upper side shows a completely homogeneous tissue-plate composed throughout of the same kinds of cells. In the majority of cases elements of different kinds take part in the composition. If we take no account of those plants in which certain epidermal cells undergo especial development as crystal reservoirs, secreting glands or idioplasto-containing cystoliths, three especially

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1. Compare for example, v. Bambeka, S. un exemplaire monstrueux de Polyporus sulfureus. Bull. Soc. Mycol. France, 1902, T. XVIII, p. 34.

2. Concerning leaves of the witches brooms on Abies, and the like, compare, below, Chapter V, B, 5.

3. Compare Costantin, Rech. s. l. Sagitaire. Bull. Soc. Bot. France, 1885, T. XXXII, p. 218.

important forms of upper-dermatogen cells, or rather of their derivatives come into question,- guard cells, hairs, and slimy epidermal cells.

An arrestment of the development of the guard cells may be brought about in various plants by well known means. Lowered transpiration and wak illumination cause a decrease of stomata. According to Stapf's count, in Solanum tuberosum , there is, under normal conditions, one stoma for every 46 epidermal cells. In the specimens which he let mature in gaslight, a pair of guard cells occurred for every 204 epidermal cells. The same reduction may be proved for shade leaves.[1]

(45) Contact with running water acts just as does retention in damp air, but often more energetically. According to Mer, leaves floating below the surfact of the water do not develop so many stomata as those which reach the surface. In some plants, finally, the formation of stomata is omitted entirely under the action of moisture. In many plants which "normally" develop air and water leaves, stomata are found only on the former; in Stratiotes the submerged part of the leaf is free from stomata, while that above the water possesses some. Stomata are entirely or almost entirely lacking in leaves of Marsilia which develop under

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1. Stapf, Beitr. zur Kenntnis d. Einfl. geänderter Vegetationsbeding. auf die Formbildung der Pflanzenorg. etc. Verh. Zool. Bot. Ges., 1879, Bd. XXVIII, p. 238. From the further statements of Stapf, we gather that in the "vapor-form" a stoma, occurred for every 50 epidermal cells, in that cultivated in a room, only one for every 113. Regular relations between the differentiation of the epidermis and the external factors may not be understood from this; only so much is clear, that the number of the stomata often decreases under abnormal cultural conditions. Dufour made observations on shade leaves (Infl. de la lumiere s. l. structure d. feuilles. Bull. Soc. Bot. France, 1886, t. XXXIII, p. 92.) and Mar (Observe s. la repartition d. stomates etc. Ibid. p. 121.) They proved that shade leaves possess fewer stomata than sun leaves. Brenner (Unters an eigenen Fettpfl. Flora, 1900, Bd. LXXXVII, p. 387) arrived at the same results in the case of Mesembryanthemum, in that, when cultivated in a damp place, 19 to 23 stomata were found, instead of 50 to 52, as in a normal leaf. It is very remarkable that in the case of other succulents under similar cultural conditions, the number of the stomata increases, (in Crassula 110 to 160 or 100 to 110, instead of 90 or 70, as in the normal leaf.) Here also were not in a position to set up any rule. Compare also the results of W. Wollny, Unters. ub. d. Einfl. d. Luftfeuchtigkeit auf das Wachstum der Pfl. (Diss.). Forsch. Gebiet Agrikultur-Physik, 1898, Bd. XX. Further literature is cited in the following references.

water.[1] To this type belongs also, I suspect, the Asplenium obtusifoluim var. aquatica, in which Giesenhagen[2] described the tissue differentiation as strongly reduced and the stomata lacking; still others might be mentioned.[3]

Conditions for the formation of hairs are similar to those for the formation of stomata. Because of the ease of macroscopic control the dependence of pubesence on climate and culture conditions found early consideration.[4] The trichomes are also arrested in development by the factors referred to. Etiolated plants, plants transpiring poorly, or those vegetating under water, develop only scanty hair coverings.[5]

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1. Costantin, Etude, s. l. feuilles s. pl. aquatiques, Ann. Sc. Nat. Bot. 1886, 7 ser., T. III, p. 94, also Infl. du milieu aquatique s. l. stomates. Bull. Soc. Bot. France, 1885, T. XXXII, p. 259. Schmidt E., Einige Beob. z. Anat. d. Vegetationsorg. v. Polygonum. Diss. Bonn 1879. Massart, L'accommodation individualle chez Polygonum amphebium. Bull. Jard. Bot. Bruxelles, 1902, Vol. I, fasc. 2.

2. Ueber hygrophile Farne. Flora 1892, (Erganzungsband) Bd. LXXVI, p. 157. Concerning leaves of the witches brooms of ferns, compare below, Chapter V, B. 5.

3. The question, whether the formation of the stomata may be suppressed by unfavorable life conditions may have been one of the first in the province of pathological plant anatomy which were taken up experimentally. In his "Anatome der Pflanzen" (Berlin 1807) Rudolph refuted the statement of De Candolle (1801) according to whose explanation, "la lumiere est encore necessaire au development des pores. Les plants etiolees n'en ont aucun." Rudolph found in etiolated leaves of Ipomoea carnea and I. violacea stomata in normal numbers, just as in the young leaves of the bamboo, of calla etc., which he had not exposed to light. In the case of the variegated leaves of Arundo Donax, A. colorata, Agave americana, etc. (which Rudolph also reckoned among etiolated ones), equal numbers of pores were found, according to him, on the gree. and one the etiolated parts of the leaves. Again Rudolph refuted the further statement of De Candolle (loc. cit) that land plants, grown under water, can no longer form stomata. Experiments with Mentha prove the opposite. "Any one who grows under water one of the plants designed to grown on dry land, will not thereby take away its pores". (Rudolph, loc. cit.)

4. Compare these textbooks from the beginning of the last century. One may here also be referred back to Goethe.

5. Some citations of literature: Kraus, C., Beob. üb. Haarbildung, sunachst an Kartoffeltrieben. Flora, 1876, Bd. LIX, p. 153; Kerner, Pflanzenleben, 1898, Bd. II, p. 449: Costantin, loc. cit. Schober, Ueb. d. Wachst. d. Pflanzenhaare an etiolierten Blatt-u. Achsenorganen. Zetschr. f. ges. Naturwiss., 1886, Bd. LVIII, p. 536; Kraus, Aug. Beitr. z. Kenn. d. Keimung. W. S. W. unter Wasser. Diss. Kiel. 1901; W. Wollney, loc. cit.

(46) With suitable objects, complete absence of pubescence may even be obtained; for instance, in potato-rsprouts, in *Polygonum amphibium,* (according to Kerner) and others.

The formation of root hairs, known to be especially sensitive objects, can also be easily arrested, or entirely suppressed. In many plants grown in water cultures, the formation of root-hairs may be omitted. In other cases we find it disappearing only in nutrient solutions of unsuitable composition. Thus Schwarz found root hairs produced in weak solutions 0.2 per cent of KNO_3, but not in strong ones, 1.5 per cent. The qualitative composition of the nutrient solution is also of great significence. Tradescantia roots remain incompletely pubescent in nutrient media free from calcium, while, in solutions containing calcium, the hairs are numbrous and well formed.[1]

The investigations of slimy epidermal cells does not furnish anything essentially new. They are lacking in the aquatic form of *Polygonum amphibium*,[2], in specimens of *Salix retusa* and *Daphne striata*, when cultivated in the moist air.[3] Their development may be arrested also by fungus infection,[4] as well as by the unknown factors causing the variegation of leaves.[5]

In the treatment of the mesophyll, however, we will take no account of relatively rare cell forms, such as crystal reservoirs, secreting glands, or stone cells and parts which store up water, but will limit ourselves to the mesophyll which has developed as assimilatory tissue. As is well known, a clearly recognizable differentiation in the layers of the latter appears in the bilaterally construc-

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1. Schwarz, Die Wurzelh. d. Pfl. Tübinger Untersuch, Bd. I, p. 135. Loew, Ueb. d. phusiol. Funktionen der Calcium- und Magnesiumsalze im Pflanzenorganismus. Flora, 1892, Bd. LXXV, p. 368. According to Dassonville (Infl. des sels mineraux s. la forme et la structure des vegetaux. Rev. gen. de Bot., 1896, T. VIII, p. 284.) the formation of hairs is omitted in distilled water. Compare with this also the statements of Pathybridge, (loc. cit.). If, according to these statements, the formation of the root hairs can be suppressed by exposure to light, we may see in this only an indirect action of the light, which is made effective by fluctuations in transpiration and turgor. Compare here, also Reinhardt, Plasmolytische Studien z. Kenntnis d. Wachstums d. Zellmembran. Festchr. f. Schwendener, 1898, p. 425.

2. Volkens, Standort und anat. Bau. Jahrb. Berl. Garten, 1885, Bd. III, p. 1.

3. Lazniewski, Beitr. z. Biol. d. Alpenpfl. Flora, 1896, Bd. LXXXII, p. 224.

4. Negar, Beitr. z. Biol. d. Erysipheen. Flora, 1902, Bd. XC. p. 221.

5. Timpe, loc. cit. Beobachtungen an *Crataegus monogyna* and *Ulmus campestris*.

ted leaves, which below the epidermis of the upper side develop one or more rows of palisade cells, and below these, several layers of spongy parenchyma. If the differentia-
(47) tion of the mesophyll is arrested, a homogenous leaf tissue is produced, composed throughout of more or less round elements resembling those of the typical spongy parenchyma, or in which the cells have developed into palisade cells, but in a lesser number of layers than under normal conditions. This arrestement of differentiation is recognizable in land plants cultivated under water, in etiolated leaves, in shade leaves, under cultivation, in too great drought or in places saturated with vapor, with the exclusion of carbon dioxide, after infection with animal or vegetable parasites, under the influence of Alpine and northerly climates and, as it seems, also under the action of other factors.[1] In all these cases, the palisade tissue disappears partially, usually, however, entirely, (compare figs. 5 and 11), and a homogenous mesophyll is produced. By the abnormal life conditions named here, the same arrestment formations, so far as leaf structure is concerned, may be obtained in very many different plants and plants of a varied nature. Still it is certain, that in plants of characteristic life habits, the normal development of many tissues presupposes also the fulfillment of special conditions. Thus, for instance, according to J. Schmidt, loc. cit., the normal leaf structure is attained only by providing the

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1. The abundant literature on this question makes more necessary than ever, a limitation to a few examples. Dufour, Infl. de la lumiere s. l. feuilles. Ann. So. Nat. Bot. VII, series, 1887, T. V. p. 311. Stahl, loc. cit. Vesque and Viet, Infl. du milieu s. l. vegetaux. Ann. Sc. Nat. Bot. VI, serie 1881, T. XII, p. 170. Lotheliar, Infl. d. l'etat hygrometrique et de l'eclairement s. l. tiges et l. feuilles d. pl. a piquants. These Lille, 1893; Rech. s. l. pl. a piquants. Rev. gen. Bot., 1893, T. V. p. 480. Mer, Rech. s. l. causes de la struct. d. feuilles. Bull. Soc. Bot. France, 1883, T. XXX. p. 110. Schmidt, J. Om ydre faktorers inflydelse paa Løvbladets anat. bygning hos en af vore strandpl. Bot. Tidske., 1899, Bd. XXII, p. 145. Costantin, Etudes, s. l. feuilles d. pl. aquatiques. Ann. Sc. Nat. Bot. VII, serie, 1886, T. III, p. 94. Schenck, Ueb. Strukturanderung submers veget. Landpflanzen. Ber. d. D. Bot. Ges., 1884, Bd. II, p. 481. Keller Biol. Studien I; Anpassungsfahigkeit phanerog. Landpfl. an. d. Leben im Wasser. Biol. Centrabl., 1897, Bd. XVII, p. 99. Duchartre, Infl. de la. secheresse s. l. vegetation et la struct. de l'Igname de Chine (Dioscorea Batatas). Bull. Soc. Bot. France, 1885, T. XXXII, p. 156. Theodorasco, Infl. de l'acide carbonique s. la forme et la struct. d. pl. Rev. gen. de Bot., 1899, T. XI, p. 445. Molliard , Rech. s. l. cecidies florales. Ann. Sc. Nat. Bot. 8 me serie, 1895, T. I, p. 67. Hartman Anat. Vergleichung d. Hexenbesen d. Weisstanne m. d. norm. Sprossen ders. Dissertation Freiburg i. Br., 1892. Leist, Einfl. d. alp. Standortes auf d. Ausbildung d. Laubbl. Mitt. Naturf. Ges. Bern. 1889, Borgesen, Bidrag til Kundskaben om arkiske Pl. Bladbygning. Bot. Tidskr. 1895, Bd. XIX, p. 219. Bonnier, Infl. de la lum. elect. continue s. la forme et la struct. d. pl. Rev. gen. Bot., 1895, T. VII, p. 241.

plants with sodium chlorid.[1]

(48) Conducting and Mechanical Tissues. Even in the discussion of the axis much may be said concerning the differentiation of the epidermis, of the assimilatory tissue in the bark, etc. In general, all that was said in the discussion of leaves also holds good here. In the same way a consideration of the conducting and mechanical tissues, which in general determine the histology of the axis, furnishes nothing essentially new. In arrested development of the axes, the vascular bundles decrease in number, the individual bundles are impoverished, the equipment with mechanical protecting sheaths degenerates or disappears entirely; instead of connected "mechanical rings", isolated groups of thick-walled elements are produced, and the collenchyma cords in the bark occur sparingly or not formed at all. The same reduction of tissue-differentiation may be obtained in roots, as in axes. In these the same factors are everywhere decisive as in the reduction of mesophyll differentiation, etc.[2] The investigations of Thouvenin deserve[3] especial mention; he retarded the development of the tissues by the action of mechanical pressure. The mechanical tissues in the stem of the Zinnia remained below the standard.

Zalenski[4] showed, further, that the length of the vascular bundles, calculated by the surface of the leaf-blade, is dependent upon external factors in such a way,

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1. Compare also the cultural experiments of Brick, Beitr. z. Biol. u. vergleich. Anat. d. baltischen Strandpfl. Schr. Naturforsch. Ges. Danzig.1888,N.F.Bd.VII,1,Heft,Glaux.

2. The above quoted authors, Bonnier, Borgesen, Costantin, Dufour, Gauchery, Hartmann, Keller, Kohl, Lothelier, Rauwenhoff, Schenck, Stapf, Teodoresco, Vesque and Viet should be compared. Compare further Perseke, Uber die Formveranderung d. Wurzel in Erde u. Wasser, Dissertation, Leipzig, 1877. Costantin. Infl. du sejour sous le sol s.l. struct. anat. d. tiges. Bull. Soc. Bot., France 1883, T. XXX, p. 230. Et. comp. d. tiges. aeriennes et sout. d. Dicotyl. Ann. Sc. Nat. Bot., 1883, VI, serie, T. XVI, p. 4. Rech. s.l. struct. de la tige d. pl. aquatiques. Ibid., 1884, VI. serie, T. XIX, p. 287. Dassonville, Action des sels. s. la forme et la structure d. veget. Rev. gen. de Bot., 1896, T. VIII, p. 284, and 1898, T. X., p. 15. Farmer and Chandler especially (on the influence of carbon dioxide etc. Proc. R. Soc. 1902, Vol. LXX, p. 413) made investigations on the influence exerted by a superabundance of carbonic acid.

3. Des modifications apportees par une traction longitudinale de la tige, C.R. Acad. Sc. Paris,1900,T.CXXX,p.663.

4. Ueb. d. Ausbildung d. Nervation b. verscheid. Pflanzen. Ber. d. D. Bot. Ges. 1902, Bd. XX, p. 433.

that in plants grown in moist places, therefore in weakly transpiring individuals, the whole length of the vascular bundles is less than in those transpiring strongly. It will doubtless be possible to demonstrate the same hypoplasia also in a comparison of the sun and shade leaves of our deciduous trees , etc.

> In the weakly grown specimens, which Daniel grew from the seeds of and Alliaria, grafted on a turnip-rooted cabbage, (Brassica Napobrassica) nothing but arrested development occurs. One will not dare, from the appearance of scanty tissue differentiation, to conclude upon a "creation des varieties nouvelles au moyen de la greffe,"[1], as Daniel attempts to do.

The study of the anatomy of blossoms and fruit and consideration of the secondary tissues can furnish further material for our consideration. Also the differentiation of anthers and anther partitions, as well as ovule and the differentiation of the fruit and seed receptacles is subject to the action of the same arresting factors, of which
(49) mention has so often been made.[2] In cambial products, arrestment in tissue-differentiation is shown by the fact that the difference in xylem in autumn and spring wood disappears, or, at least, degenerates strongly.

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1. C. R. Acad. Sc. Paris, 1894, T. CXVIII, p. 992.

2. Wieler, "(Ueb. Bezieh, zw. d. sek. Dickenwachst. u.d. Ernährungsverhältn. d. Baume. Thar. Forstl. Jahrb., 1892, Bd. XLII, p. 72) saw that the formation of the annual rings could be lacking. Kny (Eine Abnormitat in d. Abgrenzung d. Jahresringe. Sitzungsber. Naturf. Fr. Berlin, 1890, p. 138) observed thin walled autumn wood; further statements also in Verh. Bot. Ver. Prov. Brandenburg, 1879 (Ueb. d. Verdoppelung d. Jahresringe). On the anatomy of the stamens and ovules one should compare, for example, Guignard, S. l. organes reproducteurs des hybrides vegetaux. C. R. Acad. Sc. Paris, 1886, T. CIII, p. 769. Amelung, Ueb. Etiolement. Flora, 1894, Bd. LXXVIII p. 204, on the normal arrested "developments". Compare also Familler, Biogenet, Unters, üb. Verkümmerte od. umgebildete Sexualorgane, Flora, 1896, Bd. LXXXII, p. 133. The stamens of the cleistogamic blossoms in places do not develop any fibro-cells (Lecler Du Sablon, Rech. s. l. fleurs cleistogames. Rev. gen. de Bot., 1900 T. XII, p. 305. Rossler, Beitr. z. Kleistogamie, Flora, 1900, Bd. LXXXVII, p. 479).

The same arrestment in differentiation might be brought about also by exposure to weak light or the action of damp air. On arrested developments of Ovula compare also Müller-Thurgau, 2. Jahresber. Versuchsstat. Wadensweil, and still others, on arrested developments of the fruit and seed pods, compare for example, Amelung, (loc. cit.) who harvested deformed Cucurbita seed on cultures in the dark. It is well known that fruits attacked by Exoascus Pruni form no hard pit.

The question still remains to be setlled whether there is foundation and cause for giving a biological significance to the above described hypoplastic tissue formations, especially to those manifested by incomplete tissue differentiation, and to claim them as purposeful reastions of the organism to definite external agents.

In my opinion, there is no reason whatever for this. If we, first of all, confine ourselves to the "shade leaves" it is evident that their mesophyll retains, in more than one respect, the character of young, undeveloped leaves, while in the sun leaves, even these evidences are sooner or later lost by characteristic processes of growth and differentiation. According to Stahl, the mesophyll of the sun leaves of Lactuca Scariola which are oriented vertically, consists throughout of palisade cells; horizontal leaves which get the light only on the side, develop palisade cells only on the side exposed to the light, while they are entirely absent in leaves grown in shady places. Also some species of Iris do not develop palisade cells when growing in the shade. In other cases, even in shadey places, palisade cells are produced, but in a lesser development than in leaves exposed to the light. Because the characteristic palisade cells, oriented with their long axis perpendicular to the surface of the organ, are not produced, leaves grown in the shade remain similar to young, undifferentiated ones, so far as the form of their cells
(50) is concerned,[1] and besides the cells of leaves grown in the shade remind one also, in number and size, of the conditions found in undeveloped leaves. I think that the appearance of such arrested developments in no way proves the ability of the plants and leaves, "to adjust the formation of their assimilatory parenchyma, in a self-regulating manner, to the given intensity of light".[2] For this is needed primarily the experimental proof that a leaf-blade, with mesophyll free from palisade cells, is capable of a more energetic assimilatory activity in the shade, than is a leaf provided

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1. In many cases the spongy parenchyma cells of shade leaves show strong growth parallel to the surface of the leaf. As Stahl also has already indicated (loc. cit. p. 24) this stretching is to be traced back to the action of mechanical factors, and explained by the energetic growth of the leaf ribs, which stretch a little the tissue fields lying between the,. The same factors will help to explain also the porosity of the tissue in shade leaves.

2. Haberlandt. Physiol. Pflanzenanat., 2. Aufl., Leipzig, 1896, p. 253.

with palisade cells.[1] In any case, it has not yet been shown that shade leaves with their porous mesophyll structure supply the leaves with a strong transpiratory current. Geneau de Lamarliere[2] found, on the contrary, that sun-leaves transpire more strongly than shade leaves under similar external conditions. That sun leaves transpire more strongly in sunshine, that shade leaves in the shade seems a matter of course and even the scanty supplying of food substances to those leaves grown in shade explains the fact that their tissues do not develop so luxuriantly, nor are they so completely differentiated as the mesophyll of the strongly transpiring and thereby well-nourised leaves, unfolding in sunshine.

If we recognize in the formation of shade leaves, not an adjustment to definite light conditions, but only the unavoidable product of some arresting factors, the correspondence of shade leaves with leaves of plants from Alpine habitats, as brought forward by Leist, loses its remarkableness and we need no complicated explantation for the fact that land plants, placed under water, develop leaf-blades with the homogeneous structure of "shade-leaves". Schenck (loc. cit. p. 484) seems indeed to find in phenomena of the last kind also a purposeful structure adjusted to the abnormal conditions:- "the submerged plants live in a medium, which absorbs the rays of light more strongly than does the air; in a medium which places only diffuse light at the disposal of plants living in it. Water plants as well as shade plants must consequently be retarded so far as the development of the assimilatory tissue is concerned." If, however, the action of moist air is enough to produce the same homogeneous tissue structure, if the factors effective in Alpine regions, as yet insufficiently analysed but in any case not connected with weakened light,[3] can develop the same tissue form in certain plants, we will be able to attach very little value to explanatory experiments of this kind. In my opinion, up to the present, no reason exists for recognizing the mesophyll structure of shade leaves, and the parts of plants grown under water as anything other than arrested, (continued on page 50)

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1. Stahl characterized it as "right well conceivable" (loc. cit. p. 37) that with very weak light, preference will be shown for shade leaves, since the ability to bring the chlorophyll grains into the favorable position,- the horizontal position- makes possible a more productive utilization of the scanty light than can be the case in the tough sun-leaves, whose chlorophyll grains take up a position less favorable for weak light.

2. Rech. physiol. s. l. feuilles devel. a l'ombre et au soleil. Rev. gen. de Bot., 1896, Y. VIII, p, 481

3. The investigations as to the influence of Alpine life conditions on the tissue formation of plants have led to very dissimilar results in different places and in the testing of different plants. Compare especially Wagner, A., Zur Kenntn. des Blattbaues der Alpenfl. u. desen. biolog. Bedeutung. Sitzungsber. Akad. Wiss. Wien, 1892, Bd. CI.

developments. i. e. tissues scantily developed as compared with the "normal " ones.

Fig. 12, showing a cross-section through the leaf tip of the land form of Ranunculus fluitans side by side with that through the leaf of the water form, should make possible a comparison between the leaf structure of plants known as typical water dwellers, and such as become "water plants" only thruough the compulsion of the experiment, or of unfavorable external conditions. In both cases mesophyll cells of very simple round form are produced. This correspondence however, makes so much the lesss superfluous the experimental proof that the round cell functions better under such air conditions as are offered to submerged parts of plants, than do the palisade cells, since the appearance of that simple cell form shows, as we have seen, no specific effect of the diffuse light and the life under water. What complicated accessory suppositions would become necessary for the preparation of teleogical explanations, if those mesophyll structures resembling shade leaves should now be considered also in the light of appropriate reactions, produced under the influence of the too great drought, under that of a lack of carbon dioxide, upon the action of animal parasites or upon other disturbances in their nutrition?

In my opinion similar sonsiderations stand in the way also of the biological explanation of other arrested developments.

The stems of Cardamine growing under water develop, according to Schenck, no mechanical tissues; the "formation of these is unnecessary under water, for the water itself by means of its greater density keeps the plant in position favorable for light."[1] How is it, however, with those plants which mature in moist air and do not develop mechanical tissue, or indeed, with those experimental plants of Thouvenin's, although for them it would have been just as "necessary " or indeed, more than necessary than for the specimens living under normal conditions? Further through a scanty development of the medullary ray, the vascular bundles in the water form of Cardamine move somewhat toward
(52) the center, "a tendency which in typical water plants has led to the formation of axillary vascular fibres." According to Schenck such an arrangement is "purposeful" for water plants, since by this means the tensile strength of the axillary parts developing under water is increased. It may seem here as if the variation of the water form from the normal should be explained as a purposeful transformation. From my point of view, however, this cannot enter into the discussion, because keeping the plants in standing water cannot be of equal significance with keeping it in running water for only in the latter is the tension produced. Besides, the reduction of the pith, by which the vascular bundles seem shoved out of place towards the center, takes place also under other cultural conditions; for example, in strongly etiolated plants.

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1. Ueber Strukturänderung, u. s. w. Loc. Cit. p. 483.

Finally it is equally unjustifiable to deduce from conditions under which certain tissue formations cannot develop conculsions as to the functions which they would have performed under normal conditions. Tissues not developed in cultures in moist air are not thereby justified as arrangements to provide against too high transpiration. We come nearer the truth indeed through the assumption that plants in moist cultures, etc. "cannot" develop definite tissue forms, than by the supposition that the plant no longer develops these forms, because they are "no longer necessary" to it.

Taken all in all, the tissue hypoplasias as yet known, do not seem to me suitable to prove the capacity of the plant for a self-regulating adjustment to unfavorable external conditions.

We have already spoken repeatedly of the factors by which hypoplasias are produced. If we glance once more over the facts at hand, we can verify the statement that almost all of the described hypoplasias may be traced back to scanty nourishment. It is hence evident that the plants vegetating in distilled water and those cultivated in the dark or without carbon dioxid, in which we have ascertained hypoplasias, are more poorly nourished than normal ones. However, the same holds good also for the individuals which have been grown in moist places or under water, which at once, with a normal degree of transpiration, lose the supply of food substance which is necessary for normal tissue formations.

It becomes evident, especially in the higher plants, that, with insufficient nourishment, not only certain processes of growth, formation, and differentiation become impossible, but that usually a large number of varied processes also are lacking. Arrestment in the differentiation of the tissues makes itself evident not only in one tissue form of an organ, but usually in several, often in all. Only when the injurious influences are moderately effective do we occasionally find that the development of the "more susceptible" tissue forms, such as, for example, the ducts, is influenced, and that the development of those more resistant, for example, the epidermis, comes to maturity unchanged.
(53) According to our present knowledge, there are no factors which even when acting energetically, influence only one tissue form, and thus prevent normal development.

The discussion of this point seemed necessary in view of the contents of a later chapter. We will see later that, by increased utilization, the formation of individual tissues of the plant can be encouraged, while the development of others, on which no increased demands are made, does not exceed the normal amount. It would be conceivable that, as a result of abnormally weak demand upon them, those tissues forms, of which less is required, would remain below the normal in their development while the others would develop normally. It is a question whether the activity-hypoplasia, of which we will speak later in detail, lets an inactivity hypoplasia be set up in opposition to it. I have already indicated that cases of this kind are not yet known. The comparison of plants matured under water, which are supported by the surrounding medium, on which account but little is required of them mechanically, with individuals from moist cultures on which mechanical demands are made, makes it perhaps impossible (see above) to explain the omission of the mechanical tissues in the former as "inactivity hypoplasia". Besides this, all tissue forms in plants matured under water are weakly developed, just as in specimens grown in moisture or in the dark. There is no foundation for the supposition that a reduction of the mechanical tissues would result from non-utilization. For the same reasons we may not speak of "inactivity-hypoplasis" when no normal assimilatory tissue is developed in plants grown in cultures in the dark, or in places free from carbon dioxide, from which the opportunity of assimilation was taken away, etc.

Tschirch[1] explains the weak development of the mechanical ring in weeping varieties of different trees by the fact that less rigidity is required of their branches than of those of upright forms. Experimental proofs supporting Tschirch's supposition do not exist, rather, Wiedersheim's[2] new investigations make it seem impossible that the slight surplus of mechanical requisition to which the branches of upright forms occasionally the young branching ones, are subjected, could incite the branches of the weeping forms to a stronger formation of their mechanical ring. Therefore, we are not justified in terming this "inactivity-hypoplasia."

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(54) Tissue hypoplasias similar to those expressed in plants by a reduction of the cell size, decrease of the cell number and simplification of the cell and tissue differentiation, may doubtless be pointed out in the same diversity in animal organisms.

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1. Beitr. z. Kenntn. d. mechan. Gewebesystems. Pringsheim's Jahrb. f. wiss. Bot., 1885, Bd. XVI, p. 329.

3. Ueb. d. Einfl. d. Belastung auf d. Ausbildung v. Holz- and Bastkörper bei Trauerbäumen , Ibid., 1902, Bd. XXXVIII, p. 41.

Protozoa seem to offer an especially favorable material for investigation. Among others, the investigations of Maupas[1] throw light on many points of the question interesting us. In starvation cultures very numerous dwarf specimens arise, since the organisms always divide before they are "fully grown". At the same time, the processes of differentiation taking place in normal cells, are partially "arrested"; the cilia, the undulating membranes, indeed the mouth parts, are either not developed at all, or only to a reduced size. (Compare above p. 37).

In higher animals, and especially in man, incomplete tissue differentiations, corresponding to the hypoplasias above described, appear only rarely, at least, the pathological literature which I know throws only scanty light on this. As a well-known example, I will name the bones in rhactitis, in which the histological characters of the cartilage are retained longer than in normal bones. Further, tissue hypoplasia is present if succulent epithelial layers do not hornify,- and the like.

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1. Compare for example, Sur la multiplication d. infusoires cilies. Arch. zool. exp. et gen. 1888, 2me. ser. , T. VI.

METAPLASIA

After disposing in the preceding chapter of those cells or tissues which remain in some way below the normal in development, we will discuss in the following sections, those which in some way exceed the normal. In the simplest case, an abnormal advance in development may result from changes in the cell-character, without involving any increase in volume or any process of division.

The changes in cell character, exclusive of the last named processes may differ very widely among themselves. Either a breaking down of the cell content, or of a definite part of it, is involved; the organs of the cell, partially or as a whole, become incapable of functioning and die, or disappear completely. Changes of this kind are called regressive, or the transformations show that the cells perform new functions, or the cytoplasm has been increased in them, or new organs are formed, and the like. Changes of this kind are called progressive. Since inregressive changes, the symptoms of degeneration and necrosis are involved which should be kept out of our consideration, only progressive changes are to be treated of in the present chapter. We will define Metaplasia as every progressive change of any cell which is not connected with cell-growth and cell-division[1].

Since our distinction between regressive and progressive changes is based upon physiological peculiarities of the cells concerned and since, further, in judging of the latter we are often led to conclusions, the drawing of which is made possible by the anatomical character of the cells and tissues, it is evident
(56) that we will not always be able to decide with certainty whether a change in the cell body is to be termed progressive or regressive. Besides the undoubtedly progressive changes, our discussion should also take into consideration those others for which our present slight knowledge of their cell-life makes no final decision possible.

Metaplasia plays a much more modest role in the abnormal histology of plants than in the animal or human body. In the latter metaplasia from varying causes becomes the foundation of many important, pathological processes, in as much as definite tissues change their character and are transformed into other kinds, To be sure such a transition is possible only between nearly related forms, especially among the different connective tissues. Nevertheless, in metaplasia the original character of the transformed cells can become entirely unrecognizable, for example, if reticulated connective tissue be changed into fatty tissue. In plants, the number of observed transformations is very much less than in animal tissue and, moreover, in all cases the original character of the plant cells changed metaplastically remains readily recognizable. The reasons for this are not hard to find. While in the metaplasia of animal tissues the form of the cells is capable of very extensive changes, in plant cells the form remains constantly fixed by the firm cellulose covering of the individual elements. Change in form is made possible only by growth, and therefore is not involved in changes of a purely metaplastic character.

Metaplastic changes are produced in the cells of plants especially by the formation of new cell contents, or by changes of the membrane,- through growth in thickness.

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[1] So far as I know, Virchow introduced the term metaplasia.. He states that "persistency of the cells in the changing of the tissue-character, is characteristic of this process". Virchow's lecture "Ueber Metaplasie" (in s. Arch. f. path. Anat. 1884, Bd. XCVII, p. 410) is also of great interest for non-medical men.

The formation of chlorophyll in cells, which normally remain free from chlorophyll, is one of the most frequent and most striking metaplastic changes. The action of light, which, as is well-known, is indispensible for most plants in the formation of chlorophyll, often calls forth a metaplastic greening in organs which under normal conditions would have been kept from the light; tubers, bulbs, rhizomes and roots of many plants, as also the cotyledons of many seedlings, commonly germinating in the soil, become green in light. According to the prevailing theory of the production of chloroplasts we must assume that the colorless chromatophores (leucoplasts) present in the cells of underground organs are transformed under the influence of light into carriers of green coloring matter. In this connection it is worthy of note that in all underground organs only a moderate degree of green-coloration is obtainable when they become green metaplastically. Their shade differs widely from the color of typical assimilatory organs, and resembles rather the pale green of many lower or side leaves or the coleoptila of some grasses. Cotyledons of Vicia and others, removed from the stem of the seedling, become green relatively strongly when left in the light. It must be observed further that not all colorless cells and organs become green
(57) through the action of light; while the roots of Cucurbita, Menyanthes, Zea and many others may then become a pale green; the roots of other plants remain permanently colorless, pollen tubes are organs on chlorophyll-bearing plants which have never been changed to green, and they remain colorless even under the prolonged influence of light and cultivation under the most varied conditions[1]. In these and similar cases, we must for the present leave unsettled the question, whether this occurs only because the "right" combination of conditions has not yet been found which would make possible the turning green of these organs, or whether they have lost the ability to form chlorophyll, i. e., the possession of leucoplasts capable of development.

Bonnier[2] found that the tissue of his experimental plants, which were uninterruptedly exposed to the light of arc-lamps, turned green even to the pith,- the cells of the medullary rays and of the medulla, normally colorless, contained chlorophyll. But whether the appearance of the chloroplasts may be considered as an effect of the continuous exposure to light is not demonstrated with certainty by Bonnier's investigations.

Without doubt other action than that of light can induce also a metaplastic greening. The formation of chlorophyll in hypertrophied epidermal cells, which will be considered later, favors this as well as the "turning green" of corollas, anthers and ovules from the action of parasites, the treatment of which belongs to the province of pathological morphology[3].

More exact proof is still needed as to how far an increase of chlorophyll grains can be incited by the action of chemicals,

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1 The old statements of Reissek (Bot. Zeitg., 1844, Bd. II, p. 505) are based, of course, on a confusion of the pollen sacs with thread-like algae.

2 Infl. de la lumière électrique continue s. la forme et la forme d/ pl. Rev. gen. Bot., 1895, T. VII, p. 241.

3 The statements of C. Kraus, (Ueb. künstl. Chlorophyllerzeugung in leb. Pfl. bei Lichtausschluss. Landwirtsch. Versuchssta. 1877, Bd. XX, p. 415), according to which etiolated plants can be incited to the formation of chlorophyll by methyl alcohol or by mechanical arrestment of their growth in length, need testing.

especially poisonous ones. According to the investigations of Rumm and others, treatment with Bordeaux mixture causes a deep green coloration of the plants under experiment. Pethybridge makes the same statement for his wheat plants, which were cultivated in a solution containing sodium chlorid[1].

Just as in the formation of chlorophyll, a metaplastic change of the cell character can also be produced in tissues normally colorless, by the development of red pigment dissolved in the cell sap. As mentioned above (p. 38), the formation of this
(58) red pigment is dependent in many plants on the action of light and of good nutrition, and may therefore be suppressed by the removal of light and of nutritive materials. Conversely, the question must now be asked, whether the production of red coloring matter can be induced in cells, normally colorless, by the effect of light on organs which, under normal conditions, are developed in the dark, or likewise by a surplus of light, or, further, by an increased supply of nutritive material. In fact the observations on Calluna vulgaris, Azolla and many others show that especially intense lighting causes a red coloration. The same is true of many succulents (Opuntia, Sedum and others)[2]. It has been proved further that plants transferred from the plains to high mountains, often develop red coloring matter in the new habitat, supposedly under the influence of the Alpine abundance of light[3]. The same red coloration as an effect of intense lighting is conspicuous in the vegetation of the far North[4]. Finally organs which under normal conditions are kept from the action of the light, such as roots and others, are often colored red, if they are forced to live in the light (roots of Salix[5], Zea, Begonia and others).

Further the question must still be asked as to the influence of the food supply on metaplastic pigment-formation. Overton[6] has shown that in plants of the most varied kinds, the formation of red coloring matter - often indeed extraordinarily prolific - takes place if opportunity is given the plants to take up an abundance of sugar (grape, invert- or cane-). Leaves of Taraxaxum,

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1 Compare, for example Rumm: Ueb. d. Wirkung der Kupferpräparate bei Bekämpfung der sog. Blattfallkrankheit der Weinrebe. Ber. d. D. Bot. Ges. 1893, Bd. XI, p. 79. Pethybridge, Beitr. z. Kenntn. d. Einwirkung d. anorg. Salze auf die Entwickelung and d. Bau. d. Pfl. Dissertation Göttigen 1899.- Some observations on the influence of the nucleus on the growth and formation of the chlorophyll bands in Spirogyra by Gerassimoff. Abhängigkeit d. Grosse d. Zelle v. d. Menge ihrer Kernmasse. Zeitschr. allg. Physiol. 1902, Bd. 1, p. 220.

2 Compare Mohl. Vermischte, Schriften, 1845, p. 386, 390; further Askenasy, Ueb. d. Zerstörung d. Chlorophylls lebender Pfl. durch d. Licht. Bot. Zeitg., 1875, Bd. XXXIII, p. 497. Pick, Ueb. d. Bedeutung d. roten Farbstoffes bei d. Phanerogamen u. die Bezieh. ders. z. Stärkewanderung. Bot. Cbl., 1883, Bd. XVI, p. 315. DeVries, Ueb. d. Aggregation im Protoplasma v. Drosera rotundifolia. Bot. Zeitg., 1886, Bd. XLIV, p. 1 and many others.

3 Compare Kerner, Pflanzenleben, 1898, Bd. II.

4 Wulff, Th. Bot. Beobacht. aus Spitzbergen. Lund 1902.

5 Compare also Schell, Ueb. Pigmentbildung in d. Wurzeln einiger Salix-arten 95. Naturf.-Vers. Kasan. Russisch. (Just's Jahresber., Bd. V, p. 562).

6 Beob. u. Versuche üb. d. Auftreten v. rotem Zellsaft bei Pfl. Pringsheim's Jahrb. f. wiss. Bot., 1899, Bd. XXXIII,

of many Saxifrages and Crassulaceae etc., if placed in a sugar solution, color an intense red after a few days.

The red coloration appears very abundantly after injury. The edges of wounds on mutilated stems and injured leaves are often colored very intensely. First of all it remains uncertain, whether contact with the air, disturbance in the conducting paths and the consequences of these or some other factor brings about the reddening. The experiments which I made on leaves of Saxifraga ligulata are interesting. The fully grown leaves of this plant, under such life conditions as are offered in conservatories, are a succulent green, but free from red pigment. Only the younger leaves of the experimental plants were slightly reddened on the edge, as also on the underside of the larger veins. If a fully grown leaf was cut through the mid rib, a red coloration of the wound took place after a few days,- at times only after one or two weeks; but only the side of the wound toward the tip of the leaf became colored, while the opposite side remained unpigmented. It is evident that the same conditions, as regards the change of oxygen supply etc., exist on both edges of the wound. In order
(59) to explain the one-sided formation of pigment, I would like to return to the old assumption of the decreased sap flow which causes an accumulation of the food stuffs above the place of injury. The formation of red coloring matter may perhaps be explained as the result of superabundant nutrition of certain cells, just as in Overton's experiments. I would also like to propose the same explanation for the red coloration of wounds in other plants. As in Saxifraga ligulata, the accumulation of food stuffs is produced by destruction of the conducting paths and the accumulation of the contents, or, in its turn, represents the result of especial stimuli, produced after the injury. In Saxifraga ligulata, moreover, only the tissue on the veins themselves becomes red, most intensely so, immediately at the place of injury, but clearly recognizable even at a distance of 1 to 1-1/2 cm. from the wound[1].

The formation of pigment which takes place through the action of many parasitic organisms:- mostly to be sure in connection with cell growth and division, may possibly have a similar explanation. Since it is now known that even in those places a strong assimilation of proteids and starch often takes place, the possibility may be considered that here also the formation of pigment is caused by the supplying of food substances. Local reddening and early ripening under the influence of parasites was described recently by Kochs[2]. In the latter instance, the formation of pigment under the influence of light may also be traceable to nutritive factors.

Overton goes still further in his attempt to explain uniformly the phenomenon of pigment-formation. As is well known, a lowering of the temperature accelerates the reddening of many

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[1] The same independence of the red coloration on the surplus of foodstuffs, necessarily produced by destruction of the conducting paths, may be recognized in wounded or notched branches, whose leaves, according to Linsbauer (Einige Bemerk. über Anthokyanbildung. Oest. botan. Zeitschr., 1901, Bd. LI, p. 1, therein also references to the older literature), turn red above the place of injury, below it, however, remaining normally green. This distinction may be explained just as the one observed on Saxifrage leaves. Linsbauer explains the reddening very generally by the distrubances in the transference of material and explains in this way also Overton's results, "Production and transference of material stand in an entirely unusual misproportion to one another (Linsbauer)". The dissimilarity in the proportion of neighboring parts of branches and pieces of leaves above and below the normal spot is naturally not explained by this.

[2] ...fung d. Schildläuse auf d. Pflanzengew

plants. Overton calls attention to the fact that low temperatures may possibly effect an increased concentration of the sugar contained in the cell.

In conclusion, the metaplastic formations of coloring matter in the so-called graft-hybrids must be considered. Lindemuth[1], in his grafting experiments with various potato species, grafted above ground the pale green shoot of the "calico" variety with the violet shoot of the "Zebra". After 14 days the grafted axiliary part below the place of coalescence had reddened actively. It is wholly improbable that the reddening of the under part was produced by the downward conduction of the pigment; it has not yet been observed, that red pigment can wander from cell to
(60) cell. Also nothing is known of the existence of any chromogenic or leuco-connection, to which this ability to wander could be due. We would dare speak of a graft-hybrid, only if it had been made probable that the cells of the stock had been incited, by the cells of the engrafted scion, to the formation of material otherwise foreign to them. In my opinion it is, however, very much more probable that the injury, perhaps in connection with some factors effective at the time of coalescence, led to the formation of the red pigment[2]. In the described phenomena on red coloration I can discover no proof of any graft-hybrid nature of the potato plants described.

Further study of the conditions under which the development of the red pigment of the cell sap occurs is greatly desired and promises most interesting disclosures. It is still undecided whether all the phenomena of abnormal red coloration may be fully explained by the relation to nutrition discovered by Overton. I call attention to Molisch's[3] observations, according to which young plants of Barilla nankinensis and Iresine Lindeni were colored more strongly in a nutrient solution free from nitrogen, than in cultures in spring water. Overton also made similar observations.

We may conclude briefly our views in regard to the cell contents, which besides the chloroplasts, takes part in metaplastic changes. We have spoken already of the enrichment of many cells with albumen and starch under the influence of parasitic fungi or animals. Most remarkable are the accumulations of starch which Nobba observed repeatedly in his experimental plants (Polygonum fagopyrum) when unsuitably nourished. Nobbe[4] saw "a suffocating surplus of starch grains" accumulating in the parenchyma cells of leaves of plants which were insufficiently provided with chlorin. Nutrition with unfavorable potassium salts (saltpeter,

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[1] Vegetative Bastarderzeugung durch Impfung. Landwirtsch. Jahrb., 1878, Bd. VII, p. 887.

[2] Compare also the negative results of Laurent, Nouv. rech. s. la greffe de la pomme de terre. C. R. Soc. Roy. Bot. Belgique, 1900, T. XXXIX, p. 85.

[3] Blattgrün u. Blumenblau. Schr. Ver. z. Verbreitung naturwiss. Kenntn., Wien, 1889-90, Bd. XXX. Further it should be tested whether energetic ventilation of a tissue is also influential in the formation of red coloring matter. Nienhaus (Zur Bildung blauer u. violetter Farbstoffe in Pflanzenteilen, Schweiz. Wochenschr. f. Chemie u. Pharm., 1895, Nr. 1) states that in the unripe fruit of Solanum nigrum the pigment formation developed first in the places of injury and near the stomata.

[4] Ueber d. physiol. Funktion des Chlors in d. Pfl. Landwirtsch. Versuchsstat., Bd. VII, 1865, p. 371.

potassium sulphid, potassium phosphid) carried with it the same phenomena of disease, in leaves and internodes an abnormal increase of the starch content made itself felt, at least temporarily[1]. Nobba observed similar phenomena in buckwheat plants,
(61) which had been robbed of their blossoms[2]. Schimper[3] obtained the same accumulation of starch in leaves of *Tradescantia Selloi*, cultivated in nutrient solutions free from calcium. In all these and similar cases the cells are clearly unable even to develop the diastatic ferments necessary for the solution of starch.

Similar changes in the cell character will possibly be produced also by abnormal deposits of crystals; however, cases of this kind are as yet unknown to us.

2. CELL MEMBRANE

Metaplasia of the cells can be produced by changes in the cell wall, only in so far as the membrane influences the qualities of the cell by abnormal growth in thickness or by changes of its chemical character.

In the case of growth in thickness of the membrane, two kinds of thickenings should be distinguished: either the protoplasmic membrane forms characteristic thickenings of the wall by the regular formation and distribution of bordered pits, or an irregular deposit of cellulose is laid down here and there on the normal cell membrane, sometimes abundantly, sometimes sparsely, causing the production of massive lumps, or of delicate protuberances, or the like. In metaplastic changes of cell character, wall thickenings of the first kind are very rare; as yet, I know of them only in one single plant family. The second kind of cellulose deposit, which never makes any regular recognizable distribution of the newly produced material and is distinguished by an absence of bordered pits, occurs more abundantly. To be sure there exists one case in which it cannot be decided definitely whether a degenerative process is present or not.

Regular wall-thickenings and also the formation of bordered pits were observed by v. Bretfeld in different orchids[4], whose leaves were scarred, after injury, by the formation of "netted duct" cells. In leaves of *Cymbidium alcifolium*, *C. ensifolium*, *Laelia anceps*, *Epidendron ciliare*, *C. vitellinum*, *Octomeria graminifolia*, *Maxillaria pallidiflora* and *M. crassifolia*, a "layer consisting of one or more cell-layers" is conspicuous below the destroyed cells and is distinguished from common mesophyll by a massive thickening of the cell walls. These are not thickened uniformly, but contain spores of different sizes, delicately circumscribed, which taken together give the appearance of reticulated walls. The same cells occur in the orchid leaf near the vascular bundle. During the thickening of the cell walls, the cytoplasmic contents of the cell, - the chlorophyll and starch

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1 Nobbe, Schröder and Erdmann. Ueb. d. organische Leistung des K. in d. Pfl. Landw. Versuchsstat., Bd. XIII, p. 321, 386 ff. Compare besides Frank and Sorauer (quoted p. 91, Note 5).

2 Nobbe. Landwirtsch. Versuchsstat., 1865, Bd. VII, p. 385 and Bd. XIII, p. 390.

3 Zur Frage d. Assimilation d. Mineralsalze durch d. grüne Pfl. Flora, 1889, Bd. LXXIII, p. 207.

4 Ueb. Vernarbung und Blattfall. Pringsheim's Jahrb. f. wiss. Bot., 1879, Bd. XII, p. 133.

grains,- disappear and the nucleus breaks down. Later we will again refer to the "tendency" of orchids toward the formation of netted duct cells. (Chap. IV. 4).

Cellulose deposits without any regular arrangement and without bordered pits occur in very different plants and after very different kinds of disturbances.

(62) These cellulose deposits form an especial group, and are produced by the penetration of foreign bodies into the living cell. The form of the newly-produced cellulose masses is then determined not by the quality of the cells forming the cellulose, but by the form of the foreign body. As is well known, the crystals of calcium oxalate within the cells are often surrounded by a cellulose mantle, which coalesces in one or more places with the wall of the cell containing it. (Rosanoff's crystals). Other paraplasmatic cell enclosures are also surrounded at times with a cellulose covering, such as the oil drops in the cells of the Piperaceae, Aristolochiaceae, Lauraceae. Similar cellulose formation is incited in abnormal cases when fungus hyphae penetrate into the protoplast. First of all a cellulose button forms at the place of infection. Later a sheath is produced around the penetrating hypha, and passes through the whole cell as a tube, when the hypha has traversed the cell[1]. W. Magnus saw inside the cells of Neottia Nidus avis, attacked by the fungus, clumps composed of fungus and cytoplasmic fragments changing into cellulose[2].

The cellulose sheaths of cells infected by fungi here described should not be confused with the coverings which clothe the sting canal of various plant lice throughout the lumina of the cells and the intercellular spaces. Their mention may be a propos here, since they were considered earlier to be pathological cellulose structures. Millardet designated them as "bourrelets de cellulose", and Prillieux[3] made the same mistake. According to Büsgen's thorough investigations, no product of plant cells is involved in the sheath-like structures, but an excretion of the parasite, which hardens after the withdrawal of the sting from the bundle of bristles, surrounds it as a firm tube and acts as a protection[4]. The sheath substances gives distinct protein reactions.

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1 Besides DeBary, Pilze, p. 422 and Brefeld, Brandpilze, compare also Weber, Ueb. d. Pilz der Wurzelanschwellungen von Juncus bufonius. Bot. Zeitg., 1884, Bd. XLII, p. 369; Smith, The Haustoria of the Erysipheae. Bot. Gaz. ,1900, Vol. XXIX, p. 153; Jeffrey, The gametophyte of Borychium virginianum. Univ. of Toronto Studies, Nr. 1, 1898, and many others. (Jeffrey states that a sheath of cellulose is formed only in case of the permeation of the cutinized walls in the interior of the cell). Compare also the statements in W. Magnus. (Next note).

2 Studien an d. Mycorrhiza v. Neottia Nidus avis. Pringsheim's Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 205,

3 Millardet. Hist. d. princip. var. et espèces de vignes d'origine améric. qui résistent au Phylloxera, Paris, Bordeaux, Milan, 1885, p. VIII (quoted from Büsgen, see next note). Prillieux, Etudes d. altérations prod. d. le bois du pommier etc. Ann. Inst. nat. agron., 1877-1878, T. II, p. 39.

4 Büsgen, Der Honigtau, biol. Unters. üb. Pfl. und Pflanzenläuse. Jena 1890.

In other cases growth-arresting factors are involved, especially any kind of disturbances in nutrition by which a local growth in thickness of the cell membrane is caused.

Klebs[1] observed in various algae very active thickening in the restitution membrane of plasmolysed cells (Compare above p. 14). Either a uniformly thickened and distinctly striated
(63) membrane is formed all around the contracting protoplasts, or the cellulose is deposited in excess at certain places. Here and there knobbed and cone-like protuberances are formed, which project into the lumen. But it is impossible to observe that the specific differentiation of the plant cells here influenced the shape of the new cellulose formations. There often appear in cells of the same kind, elliptical or conical masses of cellulose, or masses deposited regularly on all sides of the cells[2]. We observed the same thing in disturbances of nutrition, or under the influence of factors arresting growth in the roothairs, rhizoids (compare fig. 15), pollen tubes, Siphoneae, and other algae. Large cellulose masses are produced sometimes sphero-crystalloid in form, sometimes delicately "coralloid" cones, or small branched beams, which traverse the lumen of the cell diagonally (Noll), but layers thickened with bordered pits are never found among them.

Heavy wall thickenings resembling collenchyma occur, according to Wortmann[3], in the epicotyl, epidermis and bark of Phaseolus and other plants, if they are forcibly hindered in carrying out their reaction curvatures. The thickenings occur on that side of the axis in which the cells have prepared for the reaction curvatures by an abundant accumulation of protoplasm.

According to the statements of several authors, heavy wall thickenings appear in the fundamental tissue, as in the
(64) vascular bundles of plants cultivated in nutrient solutions of

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[1] Beitr. z. Phys. d. Pflanzenzelle. Tübinger Unters., Bd. II, Heft 3 (1888), p. 489.

[2] Compare Schaarschmidt, Zellhautverdickungen u. Cellulinkörner bei Vaucherien and Charen. Bot. Cbl., 1885, Bd. XXII, p. 1. Further statements are to be found, for instance in Stahl, Ueb. den Ruhezustand der Vaucheria geminata. Botan. Zeitg., 1879, Bd. XXXVII, p. 129; Heinricher, Z. Kenntn. d. Algengattung Sphaeroplea, Ber. d. D. Bot. Ges., 1883, Bd. I, p. 433; Noll, Experim. Unters. üb. d. Wachstum d. Zellmembran. Abhandl. Senckenberg. Naturf. Ges., 1883, Bd. XV, p. 101. Zacharias, Ueb. Entsteh. u. Wachstum d. Zellhaut. Ber. D. D. Bot. Ges., 1888, Bd. VI, p. LXIII. Haberlandt, Ueb. Einkapselung d. Protopl. m. Rücksicht auf d. Funkt. d. Zellkerns. Sitzungsber. Akad. Wiss. Wien, 1889, Bd. XCVIII, Abt. 1, p. 190. Tomaschek, Ueb. d. Verdickungsschichten an künstl. hervorgeruf. Pollenschläuchen v. Colchicum autumn. Botan. Cbl., 1889, Bd. XXXIX, p. 1. Raciborski, Ueb. d. Einfl. äuss. Bedingungen auf die Wachstumsweise des Basidiobolus ranarum. Flora, 1896, Bd. LXXXII, p. 113. Sokolowa, Ueb. d. Wachstum d. Wurzelh. u. Rhizoiden. Bull. Soc. Imp. Nat. Moscou, 1897, p. 167. Lämmermayr, Ueb. eigentümlich ausgebildete innere Vorsprungsbildungen in d. Rhizoiden v. Marchantieen. Oesterr. Bot. Ztschr., 1898, Bd. L, p. 321 and many others.

[3] Zur Kenntnis der Reizbewegungen. Botan. Ztg. 1887, Bd. XXXXV, p. 785, Elving; Zur Kenntn. d. Krümmungserscheinungen d. Pfl. Öfversight Finska Vet. Soc. Förh. 1888, Bd. XXX.

two weak concentration or of unsuitable composition[1].

The above mentioned process of growth in thickness can be combined also with changes in growth of the whole cell. That is true of the netted-duct thickenings first named, as well as of the irregular cellulose accumulations free from bordered pits. We will have to return therefore in the next chapter to similar structures.

Changes in the chemical composition of the membrane as well as pathological changes of the cells, micro-chemically demonstrable, do not belong to our subject. Besides it is not improbable, that, just as in the formation of abnormal cellulose deposits, processes of a degenerative nature are involved in the production of foreign matters, which impregnate the cellulose covering and change thereby the chemical character of the cell wall. In any case the death of the cell often follows. Some few notes on suberization and lignification suffice here.

In the case of rhizomes and petiole of some ferns, a browning of the cell-wall follows an injury, which makes itself evident first in the middle cells, then also in the other layers of the cell wall. Retention in water appears, in higher plants, to cause the suberization of the superficial tissues[2]. According to Tittman[3] the exposed cross walls of the cut hyphae of Cladophora glomerata, develop a cuticle.

I observed lignification of the cell walls without noticeable growth in thickness in the leaves of Juglans under the influence of colonies of Lachnus Juglandis. The leaf lice stayed on the upper side of the leaves, in fact on the mid rib, and brought the tissue lying over the rib to lignification. Similar effects might also be caused by other parasites which do not form galls.

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1 Compare for instance, Dassonville, Infl. des sels minéraux sur la forme et la struct. des vég. Rev. gén. de Bot. 1896, T. VIII, p. 284; Pethybridge, loc. cit. Further, Stange, Bezieh. zwisch. Substratconcentration, Turgor u. Wachstum bei einigen phanerog. Pfl. Botan. Ztg. 1892, Bd. L, -. 365.

2 According to Costantin, Etude comp. d. tiges aériennes et souterraines des Dicot. Ann. So. Nat. Bot., 1883, 6me sér., T. XVI, p. 4; also Rech. s. la struct. de la tige d. pl. aquatiques. Ibid. 1884, 6me ser., T. XIX, p. 287. Sauvageau observed that in aquatic plants Potamogeton and others, the cells lining the air passage turned to cork after the intercellular spaces had been filled with water. (Sur les feuilles de quelqu. monocotyléd. aquatiques. Thèse, Paris 1891, p. 181). According to Thomas.J. (Anat. comp. et expér. d. feuilles souterraines. Rev. gén. de Bot., 1900, T. XII, p. 394) the cuticle of the under side of the leaf is more conspicuous in the cultivation of shoots bearing leaves under the surface of the ground than under normal conditions.

3 Beob. über Bildung u. Regeneration d. Periderms, d. Epidermis, d. Wachsüberzuges, etc. Pringsheim's Jahrb. f. wiss. Bot., 1897, Bd. XXX, p. 116.

4 Kochs (loc. cid.) observed lignification (metaplasia) in twigs infected by Asterodiaspis quercicola (Coccus Quercus). Part of the bark cells grow greatly in a radial direction and lignify later - others turn to wood, without any previous elongation.

CHAPTER IV.

(65) ## HYPERTROPHY.

We understand by the term Hypertrophy, an abnormal process of growth, which, with an exclusion of cell-division, leads to the formation of abnormally large cells. "Hypertrophy" to my mind", says Virchow[1], "would be the case where single elements take up a considerable amount of material. thereby becoming larger, and also where, by the simultaneous enlargement of many elements, a whole organ finally becomes distended." In the following description cases will also come under discussion, on the one hand, where only single cells hypertrophy, on the other hand, those in which all the elements of extensive cell groups enlarge and thereby bring about an hypertrophy of the tissue. The absorption of material mentioned by Virchow, has been left out of the question purposely in our definition. While in animal cells in an overwhelming majority of cases, cell growth is associated with an increase of the living cytoplasmic contents, and usually is identical with it, in plant cells, the absorption of water,- united with surface growth of the cellulose wall plays a prominent role as a phenomenon of growth. Since it is difficult to decide in many cases, whether the growth of the cells is associated with an abnormal absorption of material or not, we will designate as hypertrophy only the abnormal increase in volume of the cells,- no matter if "over-nourishment" of the cells concerned precedes the abnormal growth, or only an abundant absorption of water.

It is evident that, by the word "hypertrophy", a process is to be designated. Nevertheless, we will take the liberty following the usuage of pathologists of calling hypertrophies, the abnormally enlarged cells themselves and the tissues altered by the cell growth. The same word may serve to denote the process of growth and its tangible products.

As "hypertrophy in a wider sense of the word," many pathologists designate also the growth in amount due to an
(66) increased number of the single elements.[2] I prefer to divide them more strictly and to designate all changes as hyperplasia. (Compare Chapter V) which are allied with processes of division.

In the anatomical investigation of hypertrophies in the plant world, different ontogenstic and histological

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1. Cellularpathologie, 1858, p. 58.

2. Compare for instance, Ziegler. Allgem. Pathologie, 10, Aufl., 1901, p. 274.

points of view will have to be taken into account.

In regard to the cell-material from which the hypertrophied elements are derived various cases are conceivable: cells of the most varied kinds, belonging to the most varied tissue forms, epidermis, bark, mesophyll, vascular bundle cells, etc., furnish hypertrophies, in short, all cells which are still alive and whose membrances are still capable of growth, can hypertrophy: as is well-known, lignified membranes achieve no further surface growth.

Various possibilities are conceivable also in the production of abnormally large elements, just as before in the discussion of abnormally small cells:-

a. Either the hypertrophied cells are derived from meristematic elements which, under normal conditions, would have divided further, in which case hypertrophies are indeed produced by a continued growth of the cells, but with no further division, or only a tardy division takes place of such kind that larger daughter cells arise than under normal conditions:

b. Or cells are involved which continue longer or more intensively than under normal conditions the growth in length which follows the last division.

c. Or cells of a permanent tissue are concerned, which have previously ended their normal growths and are excited to a subsequent increase by certain external factors.

It is not always easy to decide in detail to which of the growups here named the different kinds of hypertrophies belong. The qualities of the abnormally large cells themselves never throw light upon the kind of tissue-elements, to which they may be traced back ontegenetically. In the over-whelming majority of cases, those mentioned second are involved. Obviously, the most important difference between the two modes is that the participating growth is abnormal only in the second case: in cases of the first kind, the abnormality lies alone in the omission of cell-division. Since we have already characterized hypertrophy as an "abnormal process of growth", it follows that strictly speaking we are not concerned in these with hypertrophies,- that therefore abnormally large cells can also be produced otherwise than by hypertrophy. Nevertheless, on account of the external, correspondence with products of hypertrophical growth, examples of the first named mode of development must be discussed in the present chapter.

We will now fix our attention upon the process of growth. The coefficient of increase is either equally large in all directions, or some special direction of growth may be recognized. In the first case, the old proportions of the
(67) cell changed hypertrophically will remain; the hypertrophied cell will show an enlarged picture of the normal so far as its form is regarded. In the second case, the proportions will be changed in some way, and a formal change in value must appear; for instance, a sac-like cell will come from a

round one and the like. The cases in which the cells make abnormal growth only in one direction are extraordinarily frequent. In this connection it should be noted further

that, in many cases of hypertrophy, the cell membrane will not be capable of abnormal growth in all its parts, but only on certain sides and in limited regions. In the epidermal cells, for example, in many cases only the outer wall makes any perceptible surface growth:- the form and size of the original epidermal cell remaining permanently recognizable. The added growth as well as the hypertrophied cells, as a whole, are independent, in their shape of the normal form of the original cell, and entirely different from it. (Compare fig. 45). Further:- cells which are enclosed on all sides by tissue, and indeed by tissue incapable of growth, have at their disposal only a limited space for their hypertrophic increase in volume, and only a narrowly limited region of their membrane can participate in the surface growth. Thus this added growth appears often as an independent appendage of the mother body of the cell, whereby there results, as a matter of course, a complete change in the form of the hypertrophied cell.

During, or after the increase in volume, the contents of the cells and the structure of their walls usually undergo other and various changes. The cases are relatively rare in which such changes are entirely omitted and the anatomical character of the cell remains the same. There is usually a revaluation of the cell character: either regressive changes result, the cytoplasm is used up, the cell contents degenerate or are dissolved,- or progressive changes take place, which give the cells new anatomical characteristics and functions; the cells store up proteins, starches and fats, or they develop chlorophyll and red coloring matter in the vacuoles, or their walls are thickened characteristically. In hypertrophies of the first kind, which we will designate as <u>kataplastic hypertrophies</u>, the anatomical state does not lead us to believe that the abnormal growth is produced by an increased supply of food stuffs, i.e., by "over-nutrition". On the contrary, the processes described make it often probable, that the cells are dependent on their own contents for nutritive material for the hypertrophic growth, thus exhausting it and thereby preparing their own destruction. In cases of the second kind, a combination, so to speak, of hypertrophy and metaplasia exists, we will speak of <u>prosoplastic hypertrophy</u>. In these cases, the abnormal growth often is apparently accompanied by an abundant supply of nutritive material, if not caused by "over-nutrition". Indeed in them an increase of the most important cell-organs is possible; besides the enrichment in cytoplasm there may be proved at times, an increase of the nuclei. Such multi-nucleated cells serve as transition-forms between hypertrophies and those abnormal structures, by which division of the cells usually follows upon cell growth, that is hyperplasies.

I choose the designation "<u>kataplastic hypertrophy</u>" for abnormal increase in volume of the cells connected with degenerative atrophy of their living contents with reference to the terminology proposed by Beneke .[1] Beneke designated the functional "decline of the cell" - in my opinion very fittingly - as "kataplasia". Since, in our case, the unmistakable decline is associated with increase in cell volume, it is very natural to speak of kataplastic hypertrophy.

> Evidently the abnormal processes of growth here in question are not unlike those which Roux[2] has designated as processes of "purely dimensional growth". This is not dependent on assimilation, but predominantly on the deposition of the original substance already on hand, while "growth in amount" is produced by increase of the specifically composed organic substance. In plant cells, in the last phase of their normal development, the "dimensional growth" plays evidently (compare Roux) a prominent part. The increase in amount of the cells is not caused by increase of their organic substance, but by the enlargement of their vacuoles. Also, in the cases of abnormal increase in size, designated by us as Kataplastic, a "dimensional growth" is involved, of which the products, however, are here especially characterized by the atrophy and destruction of the cell-contents.

To be sure the etiology of hypertrophies has not been cleared up for all cases. But for the majority the active external factors have already been ascertained. Hypertrophies arise in gall-formations as reactions to chemical stimuli, further as a result of excess of water, after injury and so forth. More details will be added in the discussion of the individual cases.

In a uniform consideration of life history, histology and etiology, the following division of material is advisable.

1. Most simple cases; ie., those cases in which meristematic cells (capable of division) grow out to an unusual size, after the omission of normal cell divisions.

2. Tissues of etiolated plants which, as a result of lack of light, in moist air, etc., have developed abnormally long internodes, leaf stems, etc.

3. Hyperhydric cells and tissues, i.e., those produced by an excess of water.

4. Calluhypertrophies, i.e., those arising from injuries.

5. Tyloses, ie., hypertrophies by which only a narrowly limited part of the cell wall is incited to growth, filling out hollow places already formed in the plant body.

6. Gall-hypertrophies, i.e., those produced by the poison of the vegetable or animal parasites.

69) As appendix, we will add to these the discussion of hypertrophied fungus-hyphae, root-hairs, and other cells with apical-growth.

7. <u>Multinuclear giant cells,</u> which furnish the transition to hyperplasias. In the detailed discussion, it will be shown, that those groups also are histologically well characterized for which, in the present survey, only etiological and ontogenetic characteristics have been cited.

1. SIMPLEST CASES

We will summarize as the "simplest cases" those in which abnormally large cells are derived from elements of the normal plant body which are capable of growth and division.

If, for example, the apical cell of an alga continues its growth, but all division is omitted, under the influence of abnormal life conditions, then abnormally large cells arise. We have already answered the obvious question, whether these are to be added to the hypertrophies, or, perhaps better, are to be designated as arrested developments, since the growth which led to their formation is throoughly "normal" as such and the product is essentially characterized as abnormal only by the omission of the process of division.

The external factors, whose actions bring about the production of abnormally large apical cells, may vary. Kny[1] observed that under the influence of parasites (<u>Chytridium sphacellarum</u>) the apical cells of the side branches of <u>Cladostephus spongiosus</u> discontinue their division, but continue their growth and thus swell out slub-shaped at the upper end. No changes whatever are recognizable in the cell contents. Similar phenomena of growth occur in <u>Sphacelaria tribuloides.</u>[2]

<u>Padina Pavonia</u> furnishes a further example. Specimens of the <u>dorso-ventral</u> algae, inverted so that they are exposed to the light on their morphological under-side, uncoil their spiral edge and the cells of the apical region swell out into bladder-like forms.[3]

The same changes observed on apical cells and in the cells of the apical region can occur also in other cells capable of growth and division. Our third example should also illustrate at the same time the case in which, under abnormal life-conditions, only the division of the protoplast and the formation of the cross-wall is omitted, while the

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1. Entwickelung einer Chytridiee aus der Untergattung Olpidium Sitzungsber. Naturf. Fr. Berlin, 1871,p. 93.

2. The vesicular cells of Antithamnion are not of parasitic origin but are normal forms.Compare Nestler Die Blasenzellen v. Antithamnion plumula u.s.f. Wiss. Meeresunters., N. F., 1898, Bd. III.

3. Bitter, Anat.u. Phys. v. Padina Pavonia.Ber.d.D.Bot. Ges., 1899, Bd. XVII,p. 255.

division of the nuclei takes its normal course, so that it leades to the formation of multinuclear , abnormally large cells.

(70) Nägeli[1] found a cell with two nuclei in a filament of Spirogyra orthospira var. spiralis; it was twice as long as the normal cell. Recently v. Wissenlingh[2], who brought half spoiled cultures of Spirogyra triformis to renewed luxuriant development, observed multinuclear cells in all the filaments of the new cultures. (Compare fig. 14.) The formation of cross-walls was either suppressed entirely, or only incomplete, ring-like walls, or walls formed only on one side were produced. (Fig. 14, below.) The cells contained 2, 3, 4, and 8 nuclei. In the multinuclear cells v. Wisselingh measured an average length of 397.5 u. in the largest among them 450 and 455 u. "Yet this length is comparatively small. It is less than three times the medium length of the uninuclear cells". It is not possible to state in detail what conditions were decisive for the production of the abnormally large cells in v. Wisselingh's experiments.

Gerassimoff obtained results similar to those of v. Wisselingh in the use of lower temperatures and by treatment with poisons (Chloral hydrate, ether, chloroform). The variation from the normal consisted in the fact that a cell with no nucleus and one with two nuclei were produced from an uni-nuclear cell by division, or the new cross-wall remained incomplete and divised the cell into the two communicated[3] chambers.

The production of the multinuclear spirogyra cells corresponds in all essential points with the formation of the "long rods", which Hansen has described for Bacterium Pasteurianum[4]. On double beer in a temperature of five degrees to perhaps 34 degrees C., the bacterium appears in its "normal"form : there develop short rods, 2 u. long, 1 u. wide, united in chains. If the culture of the short

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1. Pflanzenphys. Unters., 1885, Heft. I, p. 43.

2. Ueber mehrkernige Spirogyrazellen. Flora, 1900, Bd., LXXXVII, p. 378.

3. Gerassimoff. Ueber die kernlosen Zellen bei einigen Konjugaten. Bull.Soc.Imp. Natur. Moscou,1892,p.140,Ueb. ein Verfahren,kernlose Zellen zu erhalten(Zur Phys.d.Zelle).Ibid. 1896,.Further statements also concerning multinuclear cells and cells without nuclei in de Bary (Konjugaten 1858,p.2) and Strasburger (Zellbildung und Zellteilung,3,Aufl.1880,p.183.)

4. Rech.s.l.bacteries acetifantes.Travaux du Labor.de Carlsberg,1894, Vol. III.

rods is continued on a fresh nutritive substratum at 40 degrees C., the single cells grow out into long rods. In other words, the growth is continued, but the divisions taking place under normal conditions are suppressed and "long rods" are produced which can become as long as 40 u. (Compare fig.
(71) 15). If the culture of long rods is again subjected to a temperature of 34 degrees C. the previously "arrested" segmentation is retrieved, the long cells divide into a large number of short rods:- the "normal" cell-form from which we started is again formed. It would be of great interest to learn more of the fate of probable cell-nuclei in the described processes of growth and division. We will speak later of different changes of the same bacterium under similar cultural conditions.

Future experiments will have to determine whether possibly the cells of the primary meristem also may be able to grow out of similar abnormally large elements. As yet not a case of the kind is known to me.

Blazek, who studied the "influence of Benzol fumes on cell-division" in the root tips of Pisum vativum, proved[1] that, under abnormal conditions, the nuclei divide repeatedly while the division walls often are not formed, so that multi-nuclear cells are produced. If the roots are kept in a normal atmosphere, a reduction of the multinuclear cells becomes noticeable, even after only two and one-half hours. According to Blazek the nuclei of the cells unite with one another
(72) and the cells return to the uni-nuclear normal condition by "karyogamy". Confirmation of this seems to me most desirable.

To a certain extent, those multinuclear blastomeres, the production of which in the eggs of echinoderms has been studied by several experimenters, resemble the multi-nuclear plant cells here described. I refer especially to the contributions of J. Loeb.[2] By the action of mechanical pressure, under the influence of osmotic disturbances (treatment with sea-water of abnormally high or low salt content) or by artificial warming of the eggs, segmentation is omitted while the nuclear division takes its normal course. Under special circumstances, segmentation can take place later.

2. TISSUES OF ETIOLATED PLANTS.

Plants which are cultivated in the absence of light are known to make a "false growth". Falsely grown or etiolated plants are usually characterized by the slight development of their leaf-blades, and by the excessive lengthening of their internodes and petioles.

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1. Abhandl. bohn. Akad., 1902, Bd. Xi, Nr. 17, Review by Nemec in the Bot. Cbl., 1902, Bd. XC, p. 548.

2. Ueber Kernteilung ohne Zellteilung. Arch. f. Entwickelungsmechanik, 1896, Bd. II.

The slight differentiation of tissues of etiolated plants has been discussed above; their abnormally elongated organs give rise to new questions.

We have spoken already of Amelung's statements concerning "medium cell sizes". Since it was determined that organs abnormally undeveloped in size are composed, in part at least, of abnormally small cells, the supposition is obvious that abnormally large organs are composed of especially large cells. We will test this question on the elongated internodes of etiolated plants.

Highly elongated internodes, petioles, etc., consist -often if not always - of a greater number of cells than corresponding normal organs. This kind of increase of the cell-number is, however, in itself of no consequence for our consideration, since cell increase alone does not necessitate any change in structural form. (Compa re Chapter V.) Of more importance to us is the fact, that the abnormally elongated internodes are composed of larger, longer cells, than the internodes of specimens of a normal growth. Though the abnormal size of the cells, the structural form shown in longitudinal sections, becomes essentially different from the normal. In measurements of etiolated peduncles of Tulipa Gesneriana, I found the cells of the ground tissue from a third to indeed a half longer than in the normal ones; in especially highly elongated peduncles tha cells actually became on the average almost twice as long as under normal conditions. I found the same proportions in the elongated organs of other etiolated plants.[1]

(73) Of course the same is true also of plants which make an abnormal growth in moist places. According to measurements by Stapf[2], who cultivated potato plants under different conditions, the length of the peduncl epidermal cells in the forms making an abnormal growth (cellar forms) and in normal examples bore a proportion of 217 : 117, the diameter had increased only a little. The guard cells too became larger, they twist more and more strongly and at times continue their growth so far that their ends touch (compare fig. 16), and the stoma now has two separate openings. According to Brenner[3], in normal examples of Sedum dandroideum, in cross-sections of the leaf , the dimensions of the epidermial cells bear the proportion of 18 : 8, in specimens making an abnormal growth, of 27 : 12: on the surface section of 11 :4.5 and 13 :7.5 respectively, etc. In Crassula partulacea, Mesembryanthemum

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1. Compare also Koch, Abnorme Abanderungen wachsender Pflanzenorgane durch Beschattung. Berlin 1873 (Bot. Jahresber., 1875, Bd. I, p. 283) and others.

2. Beitr. z. Kenntn. d. Einfl. geänderter Vegetationsbedingungen auf die Formbildung d. Pflanzenorgane u. s. w. Verh. Zool.- Bot. Ges. Wien, 1878, Bd. XXVIII, p. 231.

3. Unters. an einigen Fettpfl. Flora, 1900, Bd. LXXXVII, p. 387. Compare also Kohl, Transpiration d. Pfl. u. ihre Einwirkung auf d. Ausbildung Pflanzl. Gew. Braunschweig, 1886.

and others, Brenner proved "that the proportion between the length and diameter of the cells was changed more in favor of of the tangential diameter, the more moist the surrounding air".[1] Often still other changes in the tissue structure of specimens cultivated in moisture are combined with these described, often papillae-like protuberances arise in the upper epidermal cells, straight forms are replaced by such as have undulating outlines[2], and so forth.

Noll[3] recently called attention to the fact that even under other conditions than those effective in the dark and in moist cultures the same phenomena of growth occur as in plants cultivated without light.
(74) Thus, with Noll, we can speak of "starvation etiolation", if the roots of Triticum, as a result of unfavorable nutriment which lacks nitrogen, are lengthened excessively. The organs of some plants experience similar abnormal effects upon infection by parasites - to name a few instances, I will mention the Euphorbiae, deformed by Uromyces, and the Anemonae infected by Pucciniae. Probably these abnormally large organs are also composed of cells of abnormal length. Very conspicuous for instance is the enlargement of the cells (epidermal) of the leaves of Sempervivum infected by Endophyllum Sempervivi, which grow out to an abnormal length.

It is common to all the pathological phenomena here cited , that in them whole organs, internodes, leaves, whole shoots, etc., everywhere undergo the same change in anatomical structure; in those now to be discussed localized excresences of single tissue layers and closely limited pathological areas will be recognizable in the hypertrophy. While in the tissues of etiolated plants, cells are involved, which, from the first stages of their development, come under the influence of abnormal conditions, and continue their growth beyond the normal boundaries,

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1. Under the same conditions which led to the enlargement of the epidermal cells in Sedum dendroideum, Brenner found that their volume decreased in S. altissimum. In general, according to his experiments, in moist air, the diameter of the cells of the leaf, i.e. of the assimilating and most strongly transpiring organs, was so lengthened that the surface communicating directly with the air was enlarged. In the cells of the petiole, this lengthening takes place principally in the direction of the axis. (loc. cit. p. 424.)

2. Compare Brenner, loc. cit. The same undulated forms occur in the "shade-leaves" (Mer. Rech. s. les. causes de la structure des feuilles. Rev. Gen. de Bot. T. IV, 1892, p. 481); Vesque made explanatory experiments (see especially S. les. causes et sur les limites des variations de structure des vegetaux. Ann. agon. T. IX, 1884, p.481, u. T.X p. 14). Further literature citations in Brenner.

3. Ueb. d. Etiolement d. Pfl. Sitzungsber. Niederrhein. Ges. Natur- und Heilkunde, Bonn, 1901.

we will be concerned in the following predominately with hypertrophies produced under the action of external factors in cells of the permanent tissue. (Divisions 3,4, 5.)

3. HYPERHYDRIC TISSUES.

We will term hyperhydric all those abnormal tissues whose formation is to be traced back obviously to an excess of water within the plant. This excess can be produced on the one hand by super-abundant absorption, on the other hand by its reduced transpiration. The decrease of this transpiration may be necessitated by the increasded humidity of the surrounding atmosphere, by which the transpiration of the plant is arrested, or by a weakening of the transpiration ability of the plant, or finally may arise after the destruction of the transpiratory organs.

It will be seen that the hyperhydric tissues form an homogeneous group not only from an etiological point of view, but also histologically:- they all arise from abnormal enlargement of the cells, for which reason they are to be included among hypertrophies. Further, among these, are entirely lacking cases in which a prosoplastic transformation of the cells (characteristic formation of the membrane) the cell-contents, etc.) is associated with the abnormal increase in volume. We see rather in the majority of cases that, in the production of abnormally large cells, their cytoplasmic content decreases and its elements already formed, such as the chlorophyll grains, gradually degenerate. Further characteristics of hyperhydric cells and tissues will be reported later.

In cases strongly affected, a division of the single elements in some plants and in certain tissues at times, follows the cell-enlargement. As all the groups and subgroups, which we have set up, may not be separated from
(75) one another by completely sharp boundaries, an inclination towards hyperplastic tissue changes manifests itself at times even in the hyperhydric tissues. Nevertheless, all hyperhydric tissues may readily be united for a common discussion in the present chapter.

a. Lenticels and bark excresences.

As is well-known, if the cuttings of willow, poplar, alder, etc. are placed in water or in moist air, more or less extensive masses of white tissue, usually very porous, are formed on the lenticels of the cuttings. Schenck[1] investigated more closely these well-known outgrowths[2] first of all on the parts of Salix viminalis growing under water.

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1. Ueb. d. Aerenchym, ein dem Kork homologes Gewebe. Pringsheim's Jahrb. f. wiss. Bot., 1889, Bd. XX, p. 566.

2. De Candolle Men s. l. lenticelles des arbres et le devel. d. racines qui en sortent. Ann. Sc. Nat. 1826, T.VII; Mohl, Sind die Lenticellen als Wurzelknospen zu betrachten? Flora, 1832, Bd. XV, p. 65.

While the air lenticels were covered by a cap of dead, brown padding cells, Schenck found "that from the submerged lenticels a white spongy tissue develops in the form of a thin plate, which might be as thick as 2mm". Schenck collected similar observations on Eupatorium cannabinum, Bidens tripartitus and various other plants.

The anatomic investigation of the masses of white tissue presents the same appearance in all cases. The outgrowths consist always of homogeneous elements, of round, or elongated, thin-walled, colorless cells, with large intercellular spaces, and often, like a kind of star-parenchyma cells, are connected with one another by the tips of short projections (compare fig. 17); - in some places they lose all firm connection with each other, and are deposited as isolated elements in porous layers on groups of cells still connected. The individual cells are always free from chlorophyll, have a thin layer of cytoplasm and a clear, abundant cell-sap, - Schenck knew the anatomical characteristics here listed; they caused him to compare lenticel outgrowths with the "Aërenchyma" found on numerous water-plants, the water lenticels, according to him "represent to a certain extent, an aërenchymatic formation in isolated places." Göbel[1], and v. Tubeuf[2] consider the outgrowing lenticel tissue as aërenchyma.

Now since this, according to Schenck, "represents a tissue, which suffices for the respiratory requirements of parts of plants remaining under water or in slime, i. e., in media in which the supplying of oxygen must be substantially difficult in comparison with that for organs found
(76) in the air",- since further the observations described later make it little probable that the lenticels which Schenck ascribed to the aerenchymatic formations of Jussiaea, Neptunia, and others, possess this function, we will rather avoid in the following their equalization with the aerenchyma and will speak only of tissues resembling aerenchyma.

Ontogenetic investigations show that lenticel-excrescences arise from normal lenticels by enlargement of the phelloderm cells, therefore, in their formation, we have to deal with hypertrophy. Devaux[3] has proven in a few instances that hypertrophy begins in the outer layers of the phelloderm and extends to both of the innermost cell layers. A new meristem is then produced from them. In other cases the cells of all the phelloderm layers, together with the bark cells lying under the lenticel, hypertrophy; the new lenticel-meristem arises then from the more deeply lying layers of the bark tissue. According to

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1. Göbel. Pflanzenbiol. Schilderungen, 1893, p. 261.

2. v. Tubeuf. Ueb, Lenticellenwucherungen (Aerenchyma) an Holzgewächsen. Forstl.-Naturw. Ztschr., 1896,p. 405.

3. Rech. s. l. lenticelles. Ann Sc. Nat. Bot. 8me ser. T. XII, 1900, p. 139.

Devaux in exceptional cases, cell-division followed the abnormal growth.

The growth of the pehlloderm cells takes place most vigorously in a radial direction,- elongated cells, similar to sausages in form, are produced, which often lose all firm connection with one another in their longitudinal walls and remain connected only by their tangential walls. They form lose cell rows, paralell to one another and arranged radially, which curve out on the surface of the lenticel-outgrowth in flat undulations, and often separate into their individual elements. In other cases the elongation in a radial direction is omitted and the cells remain spherical.

The degree of hypertrophic enlargement varies not only in different species but also in lenticels of the same species. At times the growth of the individual cells is very slight, in which case the changes of the lenticel tissue consists principally of a breaking up, or a complete maceration of certain layers. It was not investigated more closely to see how far external factors influence the mass of hypertrophic growth.

Lenticel outgrowths of the kind described may be obtained in the most varied specimens: roots and shoots bearing lenticels form in an equal degree excresences resembling aerenchyma. The lenticels of the potato tubers, the lenticels of the leaf galls of Nematus gallarum, which lives on the willow, etc., may easily be brought to the formation of excresences. The age of the lenticell-bearing organ concerned is of no importance; I found young shoots of Populus, Catalpa, Solanum tuberosum and others, cultivated in a moist place which developed lenticels and lenticel excrescences in the immediate vicinity of the growing tips of the sprouts.

The works of v. Turbeuf and Devaux throw light on the plants, on which lenticel-excresences have already been observed.

Devaux observed hypertrophied lenticels on the shoots of the following plants:

(77)

Ampelopsis quinquefolia,	Marsdenia erecta,
Acer Negundo,	Malus communis,
Alnus glutinosa,	Morus alba,
Broussonetia papyrifera,	Pelargonium zonale,
Coriaria myrtifolia,	Platanus vulgaris,
Cydonia vulgaris,	Pirus communis,
Diervilla grandiflora,	Prunus div. sp.
Daphne Gnidium	Quercus pedunculata,
D. Laureola,	Ribes rubrum,
Fraxinus excelsior,	Robinia pseud-acacia,
Ficus Carica,	Salix div. sp.
F. elastica,	Sambucus nigra,
Gleditschia triacanthos,	Spiraea lanceolata,
Hedera helix,	Syringa vulgaris,
Juglans regia,	Tilia silvestris,
Jasminum officinale,	Ulmus campestris,
Ligustrum vulgare,	Weigelia rosea,

also on roots of the following:

Aralia Sieboldii,
Cerasus avium,
Cydonia vulgaris,
Crataegus oxyacantha,
Fraxinus excelsior,
Ficus Carica,
Ligustrum vulgare,
Monstera deliciosa,
Pandanus utilis,
Populus alba.
Prunus spinosa,
Quercus pedunculata,
Qu. Suber.
Robinia pseud-acacia,
Salix Caprea,
Solanum Dulcamara,
S. Tuberosum [1]
Sambucus nigra,
Ulmus campestris.

According to Devaux hypertrophies were absent, however, in shoots of,

Araucaria Cunninghami ,
Abies balsamea,
A. Cephalonica,
A. excelsa,
Buxus sempervirens,
Cedrus Libani,
Crataegus oxyacantha,
Corylus Avellana,
Cupressus fastigiata,
Larix europaea,
Myrica Gale,
Pinus sylvestris[2]
P. maritima,
P. Pinea,
Rhus Cotinus
Rh. Glabra.

and on the roots of,

Aesculus Hippocastanum
Castanea vulgaris,
Cupressus fastigiata,
Evonymus europaeus
Juglans regia,
Sarothamnus scoparius,
Tilia silvestris,

As Devaux himself has indicated, his reports on negative results will possibly need correction in a few points. It
(78) still remains worth noticing, that lenticels have not as yet been caused to hypertrophy in the conifers, not even the large lenticels of Gingko, which v. Tubeuf and I have also investigated.

The question of the conditions, under which the lenticel-excrescences are developed deserves special consideration.

It was evident even to the earliest observers of these structures that the production of the hypertrophies here concerned is connected with the action of water. Thorough experimental proof was undertaken first by V. Tubeuf and later by Devaux. I can substantiate their results and supplement them by some new observations.

Cuttings of poplar and others, when placed in water, become covered with lenticel-excrescences, not only on the parts moistened, but also above the surface of the water. V. Tubeuf has already brought up the question whether a stimulus coming from the water is conducted upwards, or whether the action of the moist air causes the production of the

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1. Devaux means the tubers.

2. Compare Devaux, loc. cit. p. 10.

same excrescences, as are found in the parts in conact with the water. V. Tubeuf and Devaux have agreed that it is the vapor from the water, playing about the lenticels, which incites the cells to hypertrophy. Contact with water, in a liquid state is therefore not necessary, it is even sufficient to bring pieces of twigs into an atmosphere, saturated with vapor, in order to produce lenticel-excrescences.

Although in willow cuttings and in other species the lenticels grow out more luxuriantly under water than in moist air, there arise above and under the water excrescences almost equally pronounced. There are, however, a number of plants on whose cuttings the formation of the excrescences takes place more quickly and abundantly in moist air than under water. Indeed cases are not rare, in which the excrescences under water are entirely or almost entirely absent, but are formed abundantly by the action of water vapor. Contact with water in a liquid state arrests here the development of the aerenchyma-like tissue. The difference between the moistened and unmoistened parts of cuttings of Catalpa syringaefolia is very evident. These cuttings form white masses only in moist air. Cuttings of syringa and others act similarly. Excresences is omitted further under water in the root-lenticels of different varieties of Acer, while their tissue hypertrophies unusually actively in moist air. Those lenticels of the potato tubers are still to be mentioned, which form lenticel-excrescences after having been kept several weeks in moist air, but never under water,[1] and many others.

I think the supposition is correct, that in the cases mentioned, the excrescence of the lenticel tissue cannot occur under the surface of the water on account of completely suspended transpiration and deficient supply of oxygen. I am supported in this assumption by observations on cuttings of Syringa, Evonymus and others, in which the lenticels often
(79) grow out especially abundantly near the wound-surfaces,- supposedly because the supply of air creates the most favorable conditions.

It is of no consquence what external factors are decisive in the omission of the lenticel-excrescences under water. In any case, the instances described make it scarcely probable that the aerenchyma-like lenticel tissues are of significance for the plant, in that their cell connection, with its abundant interstices, makes the breathing of the plants easier even with a more difficult supplying of oxygen, as Schenck assumes with Jussiaea etc. In many cases, the aforesaid excrescences are produced where there is no lack of air; indeed in the case of many plants, their production seems to presuppose an abundant supply of air. The rejection of Schenck's explanation will be forced upon us also by a consideration of the bark excrescences described below, which correspond in more than one way with the lenticel-excrescences already described.

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1. Apparently different varieties of potatos act differently; at least, I have often vainly endeavored to obtain lenticel excrescences in moist cultures of tubers, although in other cases, under apparently similar external conditions, their formation took place very abundantly.

If we observe for some time the development of different kinds of cuttings in a saturated atmosphere, it will be seen that the formation of the lenticel-excrescences here described illustrates the first of those formations which their tissues experience under the influence of moist air. In some species, the lenticels widen into rifts running lengthwise, which expose in places the bark tissue of the cuttings and which can enlarge to several centimetres long and up to one centimetre wide. At the same time the bark swells up greatly. (Compare fig. 18.) All these changes arise from the hypertrophic growth of the bark cells. We will later speak briefly of bark-excrescences in the description of these processes of growth.

The plant, in which I could obtain experimentally the most extensive bark-excrescences is Ribes aureum. Since this species is used as stock for standard gooseberry and currant bushes and since, further, in this species the described excrescences may be observed in nature without forced experimental interference, practical workers have given repeated attention to this bark disease which Sorauer[1] designates as "dropsy")or oedema). As figure 18 shows, boss-shaped swellings are formed on the diseased twigs which at first are still surrounded by the cork-covering but later expose their inner tissues in gaping rifts. Wounds of increasing length and breadth are produced, until at last the swollen bark tissue dies and collapses. Figure 19 gives a cross-section through part of a boss-like bark excrescence still covered by cork. The parenchymatic cells of the bark have grown out into long, sac-like cells of different form and size by a perceptible growth in a radial direction, their length here
(80) and there reaches ten or twelve times their width. At times, scattered between the sacs radially arranged, may be found elements which have been stretched tangentially. The cells of the bark medullary rays also take part in the hypertrophic growth. It should therefore be observed that, not only the cells of the outermost bark layers, but all the zones even up to the wood itself, can participate in the abnormal growth.

All hypertrophied elements have become completely or nearly colorless, the chlorophyll has disappeared, the firm connection between the bark cells is lost, they are separated everywhere from one another by large intercellular spaces, the air-content of which gives the exposed bark tissue its snowy lustre; in places the tissue disintegrates completely into its individual elements. The cell walls are most delicate, the contents consist of a thin layer of cytoplasm, and a large, clear vacuole. The bark excrescences consist therefore of a tissue which corresponds in all essential points with the aerenchyma-like products of the lenticels:- a pro-
(81) nounced kataplastic hypertrophy is involved in their production. There lie here and there between the greatly enlarged parenchyma cells gropps of prosenchymatic elements which do not take part in the enlargement.

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1. Compare especially Handb. d. Pflanzenkrankh., 2 Aufl., 1886, Bd. I, p. 233.

The macroscopic symptoms, like the histological conditions vary with the degree of the disease. In the case of barks very strongly distended, I found that the young periderm cells were being stretched in the same way as those of the bark parenchymap and were growing out into sacs, oriented radially. (Compare fig. 19). The cells of the cork-meristem seem to remain unchanged. Here too, after the growth of the cells, there follows the disintegration of the tissue into its single elements.

Outgrowths similar to those on cuttings of Ribes aureum arise further, for example, on potato tuvers. At first, when kept in a moist atmosphere, the above mentioned lenticel excrescences are formed but then the cells in the neighborhood of the lenticels also hypertrophy. The cork covering cracks up in radial rifts and in places is raised slightly and falls off, producing round wounds up to ½ cm. in diameter. in which large-celled, crystalline, glistening bark tissue is visible. Finally, these areas of excrescence, proceeding from neighboring lenticels, fuse so that in the end little scales are sloughed off here and there from the potato tuber. The hypertrophied cells resemble essentially those of the Ribes cuttings already described. The normal starch content of the cells of the potato tuber has evidently been used up in the vigorous growth, and in any case the hypertrophied cells no longer contain any starch or only scanty remains of it.

In Sambucus nigra, the rupture of the bark proceeds from the lenticels; here also the young cork cells participate in the hypertrophic growth. Yet I have not seen that such long sacs come from them as in the case of Ribes. Cuttings of Gingko biloba also the lenticels of which seem incapable of forming excrescences (see above), develop bark excrescences. The hypertrophied cells, which I found in the bark of Gingko, were however, not so regularly arranged radially as in Ribes and others, but were oriented irregularly in different directions. Bark excrescences appear further in the rose and on the hypocotyl of Phaseolus vulgaris.[1] Still further they appear on Pirus malus and Pirus communis,[2] and undoubtedly

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1. Unfortunately Sorauer makes no detailed anatomical statements. Perhaps the changes which he observed are identical with those described by Perseka (Formverand. d. Wurzel. in Wasser u. Erde. Dissertaion Beipsig, 1877).

2. Compare d. Jahrsber d. Schles Centravalverins f. Gartner u. Gartenfreunde, Breslau 1881; further Atkinson, Oedema on apple trees. Rep. Agr. Exp. Sta. Ithaca, N. Y. 1893, p. 305; also Sorauer's Angaben uber Streckung der Rindenzellen (Ueb. Frostschorf an Aepfel- und Birnenstammen. Zeitschr. f. Pfl. Krankh. 1891, Bd. I, p. 137). A further statement of Sorauer's (Nachweis der Verweichlichung der Zweige uns. Obstbaume durch d. Kultur. Ibid. 1892, Bd. II, p. 142). makes it supposable, that the bark cells on the so-called fruit-wood of the pear tree are more delicate and may be brought more easily to the formation of hyperhydric excrescences experimentally than the bark of other branches of the same species.

on very many other plants, presupposing that their bark is exposed to the action of sufficiently moist air. At times, in the case of the Ribes, the hypertrophied swelling of the bark combines with abnormally increased growth of wood, the
(82) cells of which in any case seem to be elongated radially. A closer investigation of the different bark excrescences might well make known many histological details, worth considering, although essentially the same symptoms are repeated;- elongation of the parenchymatic elements of the bark, chiefly in the direction of the radius, disappearance of the cell-contents (starch, chlorophyll) and the omission of every prosoplastic cell-change.[1]

Sorauer has already treated the question as to the external factors under whose action bark excrescences arise, and has answered it experimentally[2]. According to him, the causa morbi is excess of water.

In my experimentation with Ribes aureum, I proceeded as follows:- cuttings of shoots, several years old, were put in a glass of water and also were brought into moist air. Even before the end of two weeks, the swellings described and the first rifts are produced on the parts above the water; after possibly four weeks, extensive excrescences and gaping wounds are visible;- under water, on the contrary, the bark tissue remains normal. Potato tubers acted similarly to the Ribes cuttings; on them too, the bark excrescences were produced only in moist air, not under water. In the case of Sambucus and Gingko, I frequently observed vigorous swellings on the moistened part. Observations on potato tubers proved at the same time that even uninjured organs can form bark excrescences. Since nothing is known as to whether potato tubers form bark excrescences in moist soil, since further the excrescences are absent in tubers lying in water, and since the immersed parts of Ribes cuttings retain their normal bark structure, it may be accepted at least for these objects, that abundant supply of air is one of the conditions causing bark hypertrophy. For its production, as for the formation of the lenticel excrescences, the age of the tissue is apparently of no consequence; at least, twigs of Ribes several years old as well as young shoots (according to Sorauer) form the same bark excrescences.

The processes in Sambucus shoots and Ribes cuttings described above in which even the young periderm cells share in the hypertrophic change,

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1. Perhaps plants may still be found in which the cells of the bark parenchyma are incited, under the influence of water or moist air, not only to growth but also to division, as (according to Devaux) the cells of many lenticels,- definite nutritive conditions being taken for granted in the plant under experiment. Schenck (loc. cit.), p. 568) observed abundant division of the bark-parenchyma and the collenchyma cells on the immersed parts of the stem of Artemisia vulgaris. It will be emphasized in the following section also that division often follows abnormal cell-growth in other forms of hyperhydric tissues.
2. Sorauer, Hand. d. Pflanzenkrankh, p. 235, 236.

remind one of the aerenchyma formations described by Lewakoffski[1] and Schenck (loc. cit.) in Lythrum salicaria, Epilobium hirsutum, Lycopus europaeus, and many others. Both authors found produced on the immersed part of the shoots a soft, spongy tissue the development of which Schenck
(83) followed more closely. The bark cells on the swollen pieces of the shoots are enlarge abnormally and the products of the cork meristem also have grown out into long sacs, distended radially, which leave large intercellular spaces open between them, just as in the bark cells;- essentially therefore in the plants named, a similar tissue formation is caused by contact with water as in our Ribes cuttings in moist air. Schenck named the porous tissue, furnished by the cork meristem, aerenchyma:-"the phellogen of the above swamp plants can have two positions structurally, and the one or the other will be developed according to the consistency of the medium. What acts here as cause of the stimulation? It is not very probable that the mere contact of the epidermis with water may be considered as such; it should rather be supposed, that the lack of oxygen of the inner tissues requires the development of aerenchyma by the cytoplasm of the phellogen cells." There can be no doubt in the case of the Ribes cuttings which we studied, but aht lack of air does not give rise to the change of bark and cork tissues; indeed the amount of air furnished to the parts of shoots furrowed by the rifts is evidently especially abundant and the formation of the abnormally large distended cells is lacking in the immersed pieces of twigs which are kept from a supply of air. The similarity between our bark excrescences and the aerenchyma tissues described by Schenck would therefore be a purely formal one. In the great similarity between lenticels and bark excrescences, it would be advisable to keep them separate from the typical aerenchyma tissues formed, according to Schenck's conception, by respiratory necessity. A supplementary testing of the conditions under which the cork meristem of Lythrum, etc., develops aerenchyma might not be superfluous.

b. Intumescences.

When the cell-outgrowths, which in the case of Ribes and others led to a total change of the surrounding tissue masses, occur only in very limited areas, small pustules are produced, which we, with Sorauer, will designate as Intumescences. The processes of growth by which they are produced are essentially the same as in the case of the bark excrescences discussed above, their production also presupposes the action of the same external factors, only the size proportions and the habit of growth of the excrescences differentiates it from them. Further, excrescences which we term intumescences prefer the primary

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1. Ueb. d. Einfl. d. Mediums auf die Form d. Pfl. Vergl. Bot. Jahresber, 1873, p. 594.

tissues, the bark of young shoots, the tissues of the leaves, and blossoms. Sorauer[1] has treated intumescences especially
(84) thoroughly in numerous works, in the last few years other authors have also turned their attention to them.

Intumescences are known on the branches of Eucalyptus rostrata, Acacia pendula, Lavatera, trimestris, Malope grandiflora and others. Here and there, especially on the side exposed to the sun, the bark cells are elongated decidedly in a radial direction, finally breaking through the epidermis and swelling out as spongy mounds of tissue masses. The cells of the primary bark participate in the excrescence, the cells of the medulary rays in the secondary phloem are also swollen, but only in cases especially severely diseased, so that the formation of intumescences is thus combined with processes of the kind described above. These pustules on young branches do not furnish further anything new for our anatomical consideration.

The intumescences produced on leaves deserve more attention. Here and there on the upper or lower surfaces of the blades arise small protuberances, greenish or whitish pustules of varying height and extent. The cells, by the growth of which these forms are produced, originate usually in the mesophyll layers, which are elongated perpendicularly to the surgace of the leaf (compare fig. 20) and at times attain a length amounting to two or three times the normal one. At the same time the stronger their growth, the more complete is the destruction of the chlorophyll content, the walls of [illegible] hypertrophied cells are usually delicate, the layer of cytoplasm thin, the central vacuole large. Intumescences are produced also by distinct
(85) kataplastic hypertrophy. The epidermis lying over the outgrowing mesophyll is then only raised and slightly distended, as I found in the intumescences of Epilobium hirsutum, or it is ruptured, as, for example, in the case of Cassia tomentosa (compare fig. 20). In Ficus elastica (compare fig. 21) the lower cells of the many layered epidermis are pressed together by the growing mesophyll cells and the space originally occupied by the former is finally filled entirely with mesophyll cells. The mesophyll no longer adjoins the epidermis in approximately straight lines, but in decidedly curved ones.

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1. Compare especially Sorauer, I. Handb. d. Pflanzenkrankh, 1886, 2. Aufl., Bd. I, p. 222. II. Ueber Gelbfleckigkeit. Forsch. Geb. Agrikulturphysik, 1886, Bd. IX, p. 387. III. Weitere Beobacht. uber Gelbfleckigkeit. Ibid., 1890, Bd. XIII, p. 90. IV. Ueb. d. Knotensucht des Gummibaumes. Prackt. Ratg. f. Obst-u. Gartenbau, 1890, Nr. 4. V. Mitteil. aus d. Gebiet d. Phytopathologie II: Das, symptomatische Bedeutung d. Intumescenzen. Bot. Zeitg., 1890, Bd. XLVIII, p. 241. VI. Intumescenz bei Solanum floribundum. Zeitschr. f. Pflanzenkrankh., 1897, Bd. VII, p. 122. VII. Intumescenz an Blattern (der Nelken). Ibid., 1898, Bd. CIII, p. 291, 294. VIII. Uber Intumescenzen Ber. d. D. Bot. Ges., 1899, Bd. XVII, p. 456. IX. Intumescenzen an Bluten. Ibid., 1900, Bd. XIX, p. 115. Nypels described intumescences on Antabotrys (Notes de pathologie veget. C. R. Soc. Bot. Belgique 1897, T. XXXVI, 2. p. 256), Noack on grape berries (Treibhauskrankheit d. Weinrebe, Gartenflora 1901, Bd. I, 619), etc.

A comparison of various leaves bearing intumescences showed that, in different species, hypertrophy is connected with certain cell-layers of the mesophyll. The uppermost layer of the mesophyll in Eucalyptus globulus, e. rostrata, Ficus elastica, Cassia tomentosa (compare figs. 20 and 21), etc. participate chiefly. I found that the cells of the undermost layer hypertrophy exclusively in Epilobium hirsutum. According to Sorauer, these take part predominantly in the formation of the intumescence in Vitis, as well as in Solanum Lycopersicum[1]. Sorauer found distended cells above and below in leaves of Solanum floribundium, a participation of the whole mesophyll in carnations[2], and in extreme cases, in Vitis. In many plants; (for example, Pandanus javanicus, Cattleya, Cypripedium laevigatum, Aralia palmata, Panax arborescens, Hedera, Helix, Camellia japonica), the elongation of the cells is only very slight, so that no protuberances or only very flat ones are produced. The diseased leaf then shows yellow, transparent, usually circular spots - a symptom which Sorauer has differentiated from other cases of yellow spotting as "Aurigo" (for literature, see above).

(86) We have spoken only of the mesophyll. In fact, in most intumescences, this is the only participating tissue. In some other cases, however, the epidermal cells also are changed. Dale[3] observed swellings of the epidermis on the upper as well as on the underside in Hibiscus vitifolius, and on the under epidermis in Ipomoea (Fig. 22), In the intumescence of the tomato, mesophyll and epidermis hypertrophy.

There remains to be mentioned finally the fact, that in some intumescences not only an elongation of certain cells elements occurs, but also a division of the cells. A case described by Sorauer is especially interesting. In carnation leaves not only the mesophyll cells are stimulated to cross and longitudinal division, but at times the epidermal cells also so that a cell body is formed from them. Even in intumescences of other kinds, cell division may sometimes take place. These exceptions to the rule should not prevent our treating the intumescences as a unified group nor the finishing of this discussion in the present chapter.

Intumescences on the blossoms are known as yet only for Cymbidium Lowi (according to Sorauer, loc. cit.)

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1. Atkinson: Oedema of the tomato. Rep. Agr. Exp. Sta., Ithaca, N. Y., 1893, p. 101.

2. Compare besides Sorauer, Prillieux, Intumescences s. l. feuilles des oillets malades. Bull. Sco. Bot. France, 1892, T. XXXIX, p. 370

3. Investigations on the abnormal outgrowths or intumescences on Hibiscus vitifolius Linn. Phil. Trans. B., 1901, Vol. CXCIV, p. 163. Compare further by the same author, Intumescences of Hibiscus vitifolius. Ann. of Bot., 1899. Vol. XIII, p. 622 and on certain outgrowths (intumescences) on the green parts of Hibiscus vitifolius, Proc. Camb. Phil. Soc., 1900, Vol. X, part IV, p. 192.

The question as to the external conditions by the action of which intumescences are produced, has been repeatedly treated experimentally (Sorauer, Dale.) They arise as a result of
(87) "excess of water", if the plants under experiment develop in a saturated atmosphere. According to Dale, simultaneous action of light is necessary in the case of Hibiscus; no intumescences have been formed under water.[1] According to Copeland, they may be developed on tomato-leaves by forcing water into the branches.

It is more difficult to answer the question as to what factors determine whether mesophyll or epidermis, whether the lower or upper cell layers of the leaf furnish the intumescence. From the constancy with which the undermost mesophyll cells, in *Epilobium hirsutum*, for instance, are enlarged, or the cells of the under epidermis in Ipomea, the possibility may be considered that some constant structural peculairities of the leaf release the stimulus only in certain cell-layers, or make possible a growth-reaction only for certain ones. Dale calls attention to the fact that intumescences occur on both sides of the leaves of *Hibiscus vitifolius*, which bear stomata on both sides, while Ipomea, with stomata occurring only on the underside of the leaf develops intumescences only on this side. It is indeed not improbable, that the formation of intumescences is connected with the distribution of the stomata. This is proved also by the structures of the Vitaceae, to be further treated later (p. 90). But in no case has an explanation been obtained by the discovery of these relationships which would hold true for all cases. The examples cited above have already shown this. I call attention once more to the intumescences on the leaves of *Ficus elastica* illustrated in fig. 21, which are produced by growth of the uppermost palisade cells, although, as is well known, the leaves possess stomata only on the under side. In the majority of cases differences in the position of the different cell-layers will presumably determine participation or non-participation in the intumescence. Later we will refer repeatedly to the fact that not all layers of the leaf-tissue are capable of reacting to the same stimulus in the same way.

Closer investigation is needed to prove how far the production of intumescences is caused and favored by the treatment of plants with p oisons, especially with copper salts (compare Sorauer).[2]

In connection with the intumescences, which may be produced by the arrestment of transpiration or (according to Copeland) developed by the forcing in of water, a list of similar formations may be mentioned in the following, corresponding to developmentally and histologically. Haberlandt [3] developed in-

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1. That does not exclude the fact that occasionally the formation of intumescences is incited by temporary moistening.

2. Einige Beobacht. bei. d. Anwendung v. Kupfermitteln gegen d. Kartoffelkrankh. Zeitschr. f. Pflanzenkrankh.1893,Bd. III, p. 36.

3. Ueb. experimentelle Hervorrufung eines neuen Organs bei Conocephalus ovatus Trec. Festchr. f. Schwendener, 1899,p. 104.

tumescences by destroying the organs on the leaves of Conocephalus ovalus and C. suaveolens which eleminate water. The resulting surplus of water caused the formation of intumescences. His method consisted of painting the leaves of the plants under
(88) experiment with a one per cent alcohholic sublimate solution. A few days after the poisoning of the hydrated, thick bunches of colorless hairs (compare fig. 23) were found where groups of transient glandular hairs had stood on the young, immature leav. In their production those parenchyma cells especially participated which enclose the vascular bundles.

"On a circular spot these cells are drawn out in anticlinic curves and grow into long sacs, which remain unbrokenly connected with one another at the base showing rather numerous periclinic and, in part, anticlinic divisions. First a flat conical or disc-shaped tissue body is produced, which breaks thru the overlying leaf tissue (palisade and water-tissues, epidermis). Then the upper parts of the sacs grow out into long, colorless hairs, resembling root-hairs which stand out from one another like bristles of a brush. Not infrequently distended like clubs at the free end, they possess a living cytoplasmic wall-covering with a roundish nucleus. On the edge of the disc-like tissue body several rows of palisade cells are abundantly elongated. Their chromataphores usually degenerate before this, or at most remain in the lower part of the sacs, (loc. cit. p. 109, 110)". Besides the palisade cells, those of the xylem and of the wood-parenchyma in the vascular bundles can participate in this growth. After about a week, the delicate new formations disintegrate and are replaced by excrescences on the underside of the leaf, from the epidermis and water-tissue layer of which unicellular or multicellular water blisters are produced. Haberlandt compares these with the homologous organs of Mesembrianthemum crystallinum. In my opinion, intumescences are concerned here as well as in the bunches of hairs differently
(89) developed.

These are differentiated from those earlier described by their ability to give off water. Haberlandt tries to give them an especial significance, since he considers their formation an expedient reaction of the plant, which after a loss of the normal hydathodes, "can develop entirely new organs for eliminating water, essentially different histologically, and of other developmental origin, than any occuring in the normal developmental process of the plant." I have already stated my view[1] that there is no necessity for speaking of these described excrescences as the "new organs", and I have compared the compensatory hydathodes described by Haberlandt with callus formations since the latter at times have a similar structure and can also occasionaly eliminate water.[2] More apropos is a comparison with the above described intumescences with which they also correspond etiologically. Haberlandt himself has already called attention to the similarity betwen the structures which he developed artificially, and the hypertrophies observed by Sorauer and others. The question as to whether the latter, like the compensatory organs of COno

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1. Beitr. z. Anat. d. Gallen, Flora, 1900, Bd. LXXXVII, p. 117.

2. Compare here also Mollisch, Ueber lokalen Blutungsdruck u. s. Uraschen. Bot. Zeitg., 1902, Bd. LX, p. 45.

cephalus , might be considered as expedient new structures of the injured organisms has been answered by Haberlandt. He declares that their significance as "incomplete appendages for self-regulation" may possibly be admissable. Our present knowledge of intumescences makes it seem more advisable to me to class these with "bark-excrescences" as is done in the present presentation, since they correspond with these etiologically and histologically . In my opinion, neither the intumescences nor the bark excrescences show recognizable pecularities, on the ground of which we might describe them as "expedient" functioning formations or as asdeposition toward such formations.

Prillieux[1] observed conspicuous variations from the normal in seedlings of different plants, which we will discuss later. He germinated seeds of Phaseolus, Cucurbita, etc. in hot soil, the young plants grew but little in length, becoming, however, very thick and finally deep, gaping cross-rifts appeared on them. By anatomical investigations it was found that in all tissues the cells of the hypocotyl had been greatly inlarged, that, for example, the cortical-cells measured radially four times the normal . Occasionally besides cell growth, cell division also occurred here.

I found difficulty in confirming the statements of Prillieux, since he makes only meagre statements concerning his methods. In my own experiments, pots with different kinds of germiniating seedlings were so heated in a sandbath, that the temperature of the soil was held continuously between 40 to 42 degrees Centigrade. A bell-glass protected the cultures from drying. The seedlings of Vicia stood the treatment best. Whit-
(80) ish pustules occurred finally in their epicotyl, which were produced by growth of the epidermal and bark cells, and led to a rupturing of the epidermal tissue. Presumably, however, the formation of these "intumescences" may be explained by the very abundant amount of moisture in the air (resulting from the high temperature), not by the action of the warmth itself. I would like to assume the same for Prillieux's results. Vesque[2] also made experiments with heated soil in which "carrositas" became noticeable in the plants under experiment. Finally the "bead glands" of the Ampelidaceae should be mentioned, which occur in young branches, on petioles, leaf blades, and side-leaves of many Vitis, Ampelopsis and Cissus species.[3] Their connection with the stomata is easily recognizable. The cells below the stomata grow into the air chamber and, by continued growth, push

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1. Alterations prod. d. l. pl. par la culture dans un sol sur-chauffe. Ann. Sc. Nat. Bot., 1880, 6 ser^me., T. X., p. 347.

2. Compare the remarks at the end of the chapter.

3. Compare especially Hofmeister Allg. Morph. d. Gew., 1868, p. 545; De Bary, Vergl. Anat. d. Vegetationsorg., 1877, p. 68; D'Arbaumont, Observations s. l. stomates et les lenticel-les du Cissus quinquifolia. Bull. Soc. Bot. France, 1877, T. XXIV, p. 18, 48; Solereder, System. Anat. d. Dikot, 1899, p. 253.

up the epidermis thus forming little balls, clear as glass, on the apex of which are to be found widely opened guard cells. In their formation, cell division is not of rare occurrence. It must remain doubtful, whether the "bead glands" of the Ampelidaceae may be considered as "normal" formations or whether they are to be reckoned among the abnormal ones. It is certain that lack of light and moist[1] air favor their production. The biological explanations proposed by Müller-Thurgau and Penzig[2] do not seem to me exactly satisfying.

c. Abnormal Succulence

We may speak of "abnormal succulence" when, for example, it is possible to make those plants form "fleshy" leaves which under normal conditions, such as are characteristic of leaf succulents, would develop delicate leaf blades.

Some experiments have already proved, that it is possible to force upon certain plants some pecularities of succulents by means of treatment with salt solutions. As is well known, the transpiratory power of plants decreases considerably under the influence of concentrated salt solutions. Perhaps it is the decreased elimination of water vapor which causes hypertrophic phenomena of growth in the experimental plants nourished with strong salt solutions, causing a similarity in some respects to real holophytes.

(91) We know but little concerning this last form of hypertrophic tissue. LeSage [3] developed artificial succulence of the leaves by abundant doses of sodium chloride, especially in Lepidium sativum. The cells of the mesophyll were elongated greatly, showing thereby the same disintegration of their chlorophyll contents, as has been repeatedly described for the hypertrophies of bark and mesophyll. The statements of authors, however, do not always agree, in Pethybridge's cultures the tissues of plants treated with N_aCL remained

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1. Compare especially Hofmeister in loc. cit. Further Tomaschek, Ueber pathogene Emergenzen auf Ampelopsis hederacea. Oest. Bot. Zeitg. 1879, Bd. XXIX, p. 87. Kreuz, Entwickl. d. Lenticellen an beschatteten Zweigen von Ampelopsis hederacea. Sitzungsb. Akad. Wiss. Wien. 1881, Bd. LXXXII, Abt. I, p. 228 (here also Tomaschek, Oest. Bot. Zeitschr., 1881, Bd. XXXI, p. 252).

2. Müller-Thurgau (Perldrüsen d. Weinstocks. Weinbau u. Weinhand, 1890, Bd. VIII, p. 178) sees in them organs protective against small animals. Penzig, (Ueb. d. Peldrusen d. Weinstocks u. a. Pfl. Atti Congr. Bot. Internaz. Genova, 1892, p. 237) considers them food-bodies, which are devoured by mites or the like.

3. Rech. exper. s. l. modifications d. feuilles chez l. pl. maritimes. Rev. gen. de Bot., 1900, T. II, p. 54.

below the normal in their development.[1]

In cultivation under water, Aug. Kraus[2] obtained germinating seedlings with "fleshy" leaves (Helianthus, Lepidium sativum) which were composed of abnormally large cells. Vesque[3] obtained further "carnositas" not only through cultivation in abnormally high temperatures (see above) but also by alternate watering of the plants under experiment with 5 (or 2.5) per cent. nutrient solution and distilled water. The question still remains unanswered to what extent the "fleshiness of leaves in cultures in disadvantageous nutrient solutions[4] may be considered in this connection.

In phenomena of abnormal succulence, as in tissues of etiolated plants, tissue, formations are involved by which whole organs undergo the same change in all their parts.

4. CALLUS HYPERTROPHY

When, after injury, the living cells of an organ enlarge without division, we speak of callus hypertrophy. The cells lying near the edge of the wound enlarge at times to many times their normal volume.

Just as in the abnormal structures discussed in the last division, cell-division often follows the growth of the cells after injury. Thus it is impossible to draw a sharp line between the cases which belong here and those of callus hyperplasias. We find in the same organs of the same plant species that sometimes hypertrophic growth of the exposed cells follows injury, sometimes the formation of extensive hyperplasias,- depending upon the conditions of the organs involved and the external life-conditions.
(92) In the present section, we will have to discuss those plants and plant organs which are able to develop hypertrophies after injury. We will have to consider also the conditions under which after wound stimulation those organs and tissues react with only cell-growth, which, in general, would be

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1. Compare Pethybridge and Stange (cited above p. 57) and the literature cited by Stange.

2. Beitr. z. Kenntn. d. Keimung u. ersten Entwickl. v. Landpfl. unter Wasser. Dissertation Keil, 1901.

3. Sur l. causes et s. l. limites des variations de structure des veg. Ann. agron., T. IX, p. 481 and T. X., p. 14. (Compare Bot. Cbl. Bd. XVIII, p.259).

4. Nobbe, Ueb. d. physiol. Funktion des Chlors in d. Pfl. Landwirtschaftl. Versuchsstat., 1865, Bd. VII, p. 371. Nobbe Schröder and Erdman, Ueb. d. organ. Leistung des Kaliums in d. Pfl. Ibid., 1871, Bd. XIII, p. 321. Compare for this also Sorauer, Handb. d. Pflanzenkrankh., 2, Aufl., 1886, Bd. I, p. 187 and Frank's Urteil (Krankh. d. Pfl., 2, Aufl., Bd. I, p. 288).

able after injury to develop wound-tissue by cell-division.

We find callus-hypertrophies among thallophytes as well as among higher plants. Only rarely does the histology of the cells in this abnormal growth remain similar to the original normal one. Usually a retrogressive formation of the contents takes place. Here, as in the cells of the hyperhydric tissues, the degeneration of the chlorophyll apparatus plays a large part, the cytoplasm too may often decrease noticeably. If progressive changes of the histological cell-character appear during the hypertrophy, they involve only the development of the membrane. Thus among the cases belonging here, we meet prosoplastic hypertrophies alongside of those which bear more or less distinctly the characteristics of kataplastic hypertrophy.

I obtained the most extensive callus-hypertrophies on thallophytes in the case of Padina Pavonia. Little pieces of the broad thallus were cultivated for weeks in sea-water containing sugar; the cells, laid bare by cutting, then grew out into large, nearly colorless bladders, (compare fig. 24) which always remained undivided. The walls of the hypertrophied cells were very delicate. I observed further extensive callus-hypertrophies on raggedly torn specimens of Nitophyllum uncinatum, the outer walls of the hypertrophied cells were greatly thickened. Bitter observed cone-like thickenings of the walls in callus-hypertrophies of Padina Pavonia.[1]

(93) In higher plants, at times in the tissues of the axes and leaves, it is easy to obtain callus-hypertrophies, and they have often been observed. Although in the algae above named and in some others cell-growth alone is brought about by wound-stimulus, yet in my experience, in the case of higher plants, the cells of those tissues which can furnish callus-hypertrophies are usually capable also of producing callus-hyperplasias. External and internal factors ddetermine whether only undivided abnormally large cells are produced, or wound-tissue with more or less abundant cells.

Axes

Of the axillary tissues the bark and the wood-parenchyma show a special "tendency" to the formation of callus-hypertrophies.

My observations were made mostly on cuttings of woody plants, one end of which was under water, the other extending into moist air. The bark cells of many plants are often stimulated under these conditions to hypertrophied growth. A few examples should make clear the different kinds of changes observed here.

I observed regularly in cuttings of Cytisus that, near the upper surface of the cut, the bark cells were enlarged greatly and then grew about equally vigorously in all directions. Thus roughly ball-like or weakly lobated forms were

1. Zur Anat. u. Phys. V. Padina Pavonia. Ber d. D. Bot. Ges., 1899, Bd. XVII, p. 255.

produced which resembled the cells of normal bark tissue. Large, well-preserved chlorophyll grains, lying in the hypertrophied cells, were conspicuous,- I could not observe cell-division. In all others which I investigated, the chlorophyl content went to pieces, just as in the cells of the hyperhydric tissues. Always in Fagus only single cells hypertrophied, gowing out into large, colorless, ball-like vesicles always poor in cytoplasm. In cuttings of Sambucus I found that the thick-walled cells of the collenchyma strands also participated in the hypertrophy. In the cases I have studied the surface gtowth of the membrane was restricted to the thin-walled parts. This seems to hold good also for the collenchyma cells of the Ricinus stalk which Massart[1] saw hypertrophy strongly after injury. I have never been able to observe in cuttings of this kind that collenchyma cells can be stimulated to cell-division after injury. In other plants the bark cells are chiefly elongated, furnishing colorless sacs radially arranged. A very luxuriant growth takes place, for instance, on the cut surfaces of Syringa cuttings, the hypertrophied barl cells of which are often from two to ten times as long as they are wide.

As yet I have never observed that the bark cells of woody plants, hypertrophied after injury, had undergone metaplastic changes. In future investigations exceptions to this rule may possibly be found. Combinations of abnormal growth with metaplastic changes of the cell-character are already known in callus hypertrophies of leaves and in those mentioned in the following lines.

(94) Callus hypertrophies of an unusual kind are illustrated by the tyloses which, as is well known, are produced by the outgrowth of wood-parenchyma cells after injury, thus filling the lumina of the ducts. Since only a small section of the parenchyma cell wall takes part in the surface growth during the production of tyloses, it is allowable to compare these with the hypertrophied products of the collenchyma cells mentioned above. However, the tyloses differ so essentially from all other callus-hypertrophies, histologically and etiologically, that they may be reserved for special consideration in the next section.

Leaves

Leaves of the monocotyledons and dicotyledons,- especially of the former,- often form after injury very voluminous hypertrophies, from the exposed layers of their mesophyll. Fig. 25 shows how far the growing cells may in this way exceed their original volume. Thus the character of the cells is changed generally, in the usual way, by the disappearance of its cytoplasmic content and the disintegration of the chlorophyll, without the development of new anatomical characters. An exception worth noticing is made by Cattleya, doubtless also by still other orchids. The cells on the edge of the wound, illustrated in figure 25, form reticulated thickenings

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1. La cicatrisation chez l. vegetaux. Mem. cour, etc. Acad. Belgique, 1898, T. LVII, p. 44.

of the membrane, as is shown more highly magnified in fig.
(95) 26. In the lower part of the cell, these are only narrow meshes between the single thickened bands, which also are strongly developed.- in the upper part the bands are usually flatter and sometimes partly interrupted. This case is of special interest since, aside from the tyloses, it is the only one known to me in which hypertrophic growth, incited by wound stimulus, is combined with the formation of a special kind of wall-thickening. Unfortunately I lacked opportunity for investigating a larger number of other orchids as to their callus-hypertrophies.[1]

Miehe[2] has found in Tradescantia virginica an object of which the epidermal cells may easily be caused to form callus-hypertrophy. If, by any kind of interference, cells or cell groups of the epidermis are killed or destroyed, the empty places thus produced are filled out by the living neighboring cells. By growth, flat swellings are produced on them, which grow into the dead cells. The cavity is finally closed, since all the neighboring cells hypertrophy in the same way, and the cas formed from them lie close up-
(96) on one another. (Compare fig. 27). If a single cell closes the wound, this hypertrophying cell can reproduce the normal appearance almost completely. Its growth reminds one of the processes which were described above in the "restitution of the tissue". Even the guard cells can share by growth in the closing of the wound. While normal cells are perhaps 0.18 mm. long and 0.03 mm. broad, Miehe found hypertrophying ones become from 0.38 to 0.43 mm. long and 0.08 mm. broad. Cell-division was not observed anywhere but it may occur occasionally in Allium nutans, in which Miehe observed similar regeneration processes.

Among callus-hypertrophies I include also the abnormally large cells which Haberlandt[3] recently obtained in a culture of isolated tissue elements. Isolated mesophyll cells from the upper leaves of Laminum purpureum kept alive for weeks in Knop's nutrient solution or in nutrient fluids containing sugar and grew perceptibly at the same time thickening their membranes either on all sides or only in places. Haberlandt's statements concerning the action of the chlorophyll grains are especially interesting, In Knop's nutrient solution, they

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1. The tendency of many orchids to the formation of reticulated membrane thicking, as proved by v. Bretfeld (see above p. 61), makes probable a positive issue for further testing. It seems to have escaped v. Bretfield's attention that the formation of the described thickenings of the wall can be combined with luxuriant hypertrophic growth. I surmise that the occurrence of metaplasy or prosoplastic hypertrophy depends on external conditions. Cultivation in a noist atmosphere might here, as so often, cause or favor the production of abnormally large cells. Through lack of material, I could not test this question further.

2. Ueb. Wanderungen d. pfl. Zellkernes.Flora,1901,Bd. LXXXVIII, p. 105.

3. Kulturversuche mit isoliertin Pflanzenzellen Sitzungsber. Akad. Wiss. Wien, 1902, Bd. CXI, Abt. I, p. 69.

become gradually smaller, assumed a yellowish tinge and were transformed finally into very delicately contoured, small leucoplasts. When kept in a one per cent. sugar solution, they decrease a little in size, but keep their color; in stronger concentration (3 to 5 per cent.) they remain as large and as richly pigmented as before and often become more intensely green than they were originally. Therefore
(97) those same changes may appear in the culture of cells in inorganic solutions, which we have found to so often occur in hypertrophied cells within normal tissues. Future investigations will determine, whether it is possible to bring to hypertrophy cells left in the tissue and then, by a simultaneous supplying of carbohydrates or other nutritive substances, to prevent the retorgression of their chlorophyll contents. Haberlandt assumes that, in isolated cells, the chlorophyll grains thrown upon their own assimilation activity cannot be kept intact, since they give up their assimilatory products to the other cell-organs. Isolated assimilatroy cells of <u>Eichornia crassipes</u> soon lost their chlorophyll contents in the dark, if at the beginning of the experiment they contained no starch, "while they remain intact if, in case of scanty or insignificant growth of the cells, they can make use at least partially for themselves of the starch stored up in them". Haberlandt obtained also giant cells with thickened walls in the culture of fragments of staminal hards of Tradescantia.

Winkler (Bot. Zeitg., 1902, Bd. LX, Abt. 2, p. 264) promised further communications concerning the fate of isolated cells.

The <u>conditions</u>, under which the abnormally large cells, termed callus-hypertrophies, are produced, are still unknown to us. Of the diverse new conditions which an injury creates for the exposed cell, it has not yet been possible to separate the stimulating ones from the ineffective, nor to recognize the significance of the single factors by comparative experimental studies of their specific effects. More accessible for experimental research is the problem, under what conditions tissues of the same kind may be stimulated by injury to hypertrophic or to hyperplastic changes. Doubtless humidity plays a large part here; air containing much water vapor promotes extensive undivided growth, after injury to living tissues, just as in the case of hyperhydric ones. One of Massart's experiments (loc. cit.) supports this. He so split a stem of Ricinus by lateral pressure that two slits were opened towards the pith-cavity, two others toward the outside. (Compare fig. 28). In the slits f. f. opening towards the outside, the exposed tissues reacted with abundant cell-division; in f' f', on the contrary, only callus hypertrophies appeared. Massart assumes that contact with the open air makes possible the extensive reaction in the first named slits. A comparison with different researches makes it seem certain to me that the effect of moist air, which we may presuppose to be present in the pith-cavity of the stem, was
(98) the essential condition of Massart's experiment. The significance of transpiration lies supposedly in the fact that a more

abundant current of nutritive substances flow to the cells in which a moderately vigorous elimination of water vapor is possible. The differences, often shown by the comparison of different examples of the same species under similar external conditions, might be based upon dissimilar conditions of nutrition of the objects under investigation.

Experimental investigations into the influence of abundant nutrition on growth and cell-division have led as yet to no positive result. At least, Haberlandt was not able to bring isolated cells to celldivision by supplying abundant nutritive substances (cane-sugar).

Recently Winkler reported in a preliminary statement (loc. cit.) that isolated cells could be stimulated to division by means of poisonous substances; isolated root-parenchyma cells of *Vicia Faba* grew out to two or three celled threads, if 0.002 per cent. $CoSO_4$ was added to the nutrient solution (Knop plus 1 per cent. cane-sugar).

5. TYLOSES

As tyloses are usually designated all those spherical pouches found in the lumina of the ducts and tracheids of various vascular plants. They are known to be produced by the growth into the lumen of the ducts of the adjacent parenchyma cells through the thin-walled parts upon which they touch. The parenchyma cells do not divide - with very rare exceptions - so that we can consider tyloses to be hypertrophies.

Tyloses are distinguished from other hypertrophies, first of all, by the fact that in their production only a limited part of the membrane of the participating cells is enlarged by surface growth. The position of these narrowly bounded, growing membrane areas is determined by the releif outline of the adjacent wall of the duct. In this way only those parts of the parenchyma cell wall distend, which do not lie under resistant, thickened membranous parts of the ducts. Therefore, this explains forthwith the fact that the form-proportions of the cells producing tyloses are perceptibly changed during the growth, so that the hypertrophied cell is not an enlarged reproduction of the normal one. The cylindrical or spherical parenchyma cells acquire one or more spherical or sac-like elongated outgrowths, often of considerable size. Not infrequently the volume of the original cells remains far below that of this newly produced appendage. (Compare fig. 31). The tyloses are further characterized by the fact that they fill out hollow places already existing in the plant body. Thus, by the hypertrophy of certain cells, in the case of tyloses formation, there is brought about neither increase in volume, nor change in the form of the organs concerned, nor does it cause the formation of pustules or swellings.

All larger cavities found in the plant body,- the lumina of the ducts, the air chambers of the stomata and the secretion cavities, may indeed be filled up by hypertrophic
(99) growth of the living, adjacent cells. We will summarize as tylose-formation all hypertrophies characterized by localized surface growth of the membranes filling out any cavities in

the plant body and will describe them briefly in the following.

1. The <u>duct tyloses</u> are best known:- They are the ones which fill the lumina of the ducts and tracheids and are produced by hypertrophy of the living parenchyma cells lying in the wood.

> The knowledge of duct tyloses dates back to Malpighi, who found "oval and translucent little sacs" enclosed in the ducts of Quercus.[1] The unnamed author in the Botanische Zeitung[2] investigated their anatomy carefully. In his statements the development of tyloses from parenchyma cells is excellently described. Böhm[3] sought to explain the production of the tyloses, first of all, by an accumulation of cytoplasm between the lamellae of the duct walls, whose innermost layer grows out to form the membrane of the tylose cell. He traced it back later to an excretion of protoplasmic drops and their subsequent hardening.

The form of the tyloses is determined in the first place by the nature of the thickening of the duct wall. If ring-like thickenings are present the adjacent parenchyma cells may produce a broadly-based outgrowth into the lumen of the duct. (Compare fig. 29). The conditions in the spiral ducts are similar, if the single spirals are not too flat, and the thin membrane places are not too narrow. (Compare fig. 30). If the ducts have bordered pits, only very narrow entrances into the lumina of the ducts lie at the disposal of the growing parenchyma cells. The body of the original cell and the
(100) newly produced appendage are then united only by a narrow isthmus. (Compare fig. 31). The form of the tyloses depends still further upon whether the parenchyma cells grow out into the lumen of the duct, forming only one tylose for each cell (fig. 31) or several at the same time (figs. 29 and 30) whether therefore one or more appendages are produced on one and the same parenchyma cell. Further, the space available in the interior of the duct is of importance. Usually many tyloses push against one another in the same duct and fill the lumen with a pseudo-parenchymatic tissue, while they are flattened against one another making necessary a polyhedric form. (fig. 31). If the number of tyloses is small, they fill the lumen of the duct, as round bladders or cylindrical sacs. Complicated forms arise, if the tyloses grow out from one

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1. Anatome Plantarum, 1675-1679, Tab. VI, Fig. 21. Compare the translation by Mobius, Klassiker d. exakten Wissensch. Herausgeg. v. Ostwald, 1901, Bd. CXX, p. 7, 32.

2. Unters üb. d. zellenartigen Ausfüllungen der Gefässe, in place mentioned, 1845, Bd. III, p. 225.

3. Ueb. Funktion und Genesis d. Zellen in d. Gefässen des Holzes. Sitzungsber. Akad. Wiss. Wien, 1867, Bd. LV, Abt. II, p. 851. Ueb. d. Funktion d. vegetabil. Gefässe. Bot. Zeitg. 1879, Bd. XXXVII, p. 229.

duct into another one, as Tison[1] shows in Hamamelis virginiana.

The size of the tyloses is greatly dependent upon the space at their disposal. They sometimes grow out into cut sducts, and then attain a considerable size. I have seen them grow to gigantic sacs on the cut surfaces of Platanus cuttings and incompletely cover the exposed surface of the wood.

(101) Content and wall of the parenchyma cells, developing tyloses, remain essentially unchanged in the case of tylose formation. The nucleus of the parenchyma cell does not divide (compare the footnote). Often it wanders over into the tylose Usually the young tyloses seem to lack nuclei, since the nucleus leaves the mother cell only in late stages of tylose development.[2] The membranes of tyloses, as is true in many other hypertrophies, are often very thin! In other cases, massive thickenings of the walls may be observed and even corresponding bordered pits on the contact surfaces of adjacent tyloses (fig. 31). Möller[3] found very thick wall tyloses with the habit of growth of stone cells (stone tyloses) in the wood of Piratinera guianensis, Molisch (loc. cit. p. 273), in Mespilodaphne Sassafras (compare fig. 32.) In the case of Piratinera all the tyloses have become stone-cells, the ducts being completely stopped up with them. By this means "the homogeneity of the wood is significantly increased" (Molisch). In Mespilodaphne the stone-tyloses alternate with relatively thin-walled ones. (COmpare the figure). The wood-parenchyma cells of Mespilodaphne, developing tyloses, are otherwise rather thin-walled.

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1. Rech. s. la chute d. feuilles chex l. Dicotyl. These Caen, 1900.

2. Molisch has shown already (Zur Kenntnis d. Thyllen, nebst Beob. u. Wundheilung in d. Pfl. Sitzungsber. Akad. Wiss. Wien, 1888, Bd. XCVII, Abt. I, p. 264), that the relations between the growth of the cell wall and the position of the nucleus in the cell, which Haberlandt proved for many cases (Ueb. die Beziehungen zw. Funktion und Lage des Zellkerns, Jena, 1887) are not always recognizable in the formation of tyloses. Similar cases, however, are not lacking in which the nucleus at first remains at a distance from the distensions of the cell, produced by superficial growth of the walls and wanders over into the appendage only when it is finished, as, for example, in the haustoria of the Erysipheae, which obtain their nuclei only after concluding growth. The neucleus forces itself in to the lumen of the haustorium through the thin neck of the latter. (compare Smith, The Haustoria of the Erysipheae. Bot. Gaz. 1900, Vol. XXIX, p. 153, 167); further in the young basidia of the Basidiomycetes according to Maire (S. l. cytologie des Gasteromycetes. C. R. Acad. Sc. Pairs, 1900, T. CXXXI, p. 1246). According to K. Tamba (Die Herkunft der Zellkerne in den Gefassthyllen von Cucurbita Sitzungsber. Phys. Mediz. Soc. Erlangen, 1887, Bd. XIX, p. 4) the nucleus divides at times in the parenchyma cells of Cucurbita producing tyloses, one of the daughter nuclei goes over to the tylose, the other remains in the mother cell. Closer testing would be much desired.

3. Rohstoffe des Tischler- und Drechslergewerbes. 1883, Bd. I, p. 143.

As regards their contents, many tyloses correspond to wood-parenchyma cells, in that they store up abundant starch. Molisch found tyloses containing starch in Aristolochia, Asarum, Robina, Maclura, Vitis, Ampelopsis, Morus, Cuspidaria, Laurus, Ochroma, Sparmannia, Ficus and Ulmus, so abundantly in the rhizomes of the Aristolochiaceae, that the ducts seemed in places to be plugged up with starch.[1] Crystals, as contents of tyloses, are of little importance. The tyloses of Sideroxylon cinereum often contain one crystal, more rarely those of Maclura tinctoria, Piratinera guianemsis Loxoptergium Lorentzii, and Vitis[2] Molisch found tyloses of Ulmus filled with calcium carbonate. In regard to wound gums contained in the tyloses, refer to the statements of Will.[3]

(102) Among the most important characteristics of tyloses is the fact that they are unicellular. Despite the extent which they often attain, cell-division is omitted in almost all cases. Molisch has disproved the statements of de Bary.[4] (loc. cit.) Trecul, Gris[5], and others, who thought they had observed a separation of the tyloses from the mother cell. Molisch could prove multicellular tyloses only in the exceptional cases of Cuspidaria pterocarpa and Robina. Thorough proff is needed of the statements of Stoll[6] that the wood in Passiflora quadrangularis takes part in callus formation by means of tyloses. He says that these after repeated division, fill out the lumen of the duct near a wounded surface with a tissue that finally presses out over the cut surface.

The distribution of tyloses in ducts is almost universal in vascular plants. They are found in the parts of

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1. Compare here also Reess Für Kritik d. Böhm ' schen Ansicht ub. d. Entwickelungsgesch, und Funktion der Thyllen Bot. Ztg. 1868, Bd. XXVI, p. 1.

2. Molisch, loc. cit. p. 275 and Vergl. Anat. d. Holzes der Ebenaceen u. ihrer Verwandten. Sitzungsber. Akad. Wiss. Wien, 1879, Bd. LXXX, Abt. I, p. 65.

3. Ueb. d. Sekretbildung im Wund- u. Kernholz, Arch. f. Pharmacie, 1899, Bd. CCXXXVII, p. 369.

4. Vergl. Anat. dl Vegetationsorg, p. 178.

5. Trecul, Rech. s. l'origine d. bourgeons adventifs. Ann. Sc. Nat. Bot. 1847, 3me ser., T. VIII, p. 273. Gris, Sur la moelle des pl. ligneuses. Ibid., 1872, 5me ser. T. XIV, p. 34.

6. Ueb. d. Bildung des Callus. Botan. Zeitg., 1874, Bd. XXXII, p. 737.

various plants above ground as well as in those under ground, (rhizome, roots), but, to be sure, not in the same abundance in all families. The representatives of many a group of the plant kingdom are directly characterized by their "tendency" to abundant tylose formation such as the Scitamineae, Laurineae, Juglandaceae, Salicineae, Urticaceae, Moraceae, Artocarpaceae, Ulmaceae, Anacardiaceae, Vitaceae, Cucurbitaceae, and Aristolochiaceae. In other families, only single genera have the capacity for forming tyloses (for example, Robina among the Papilionaceae), in still others tylose formation is very rare or is entirely lacking. (Ebenaceae, Acerineae, Mimoseae, Rosaceae.

I repeat here the list of plants bearing tyloses as given by Molish in a somewhat more extended forma and limit myself therein to the statement of the generic names.[1]

(103)

Abies (Raatz)	Carica
Achyranthes	Carya
Aesculus (Maule, Tison)	Cassica
Alnus (Tison)	Castanea
Ampelopsis	Catalpa
Aralia	Celtis
Aristolochia(cf. also Tison)	Chilantus
Artocarpus	Cladrastis (Tison)
Arundo	Coccoloba
Asarum	Coleus
Banisteria	Convolvulus (Dutailly)
Begonia	Cornus (Maule)
Betula	Corypha
Bignonia	Cucumis
Boehmeria	Cucurbita
Broussonetia	Cuspidaria
Bryonia	Dahlia
Canna	Diospyros

1. Besides the literature already city, compare also the following works;- Unger, Ueb. Ausfüllung alternder u. verletzter Spiralgefässe durch Zellgew, Sitzungsb. Akad. Wiss. Wien, 1867, Bd. LVI, Abt. I, p. 751. Dutailly, Sur quelgu. phenom. determ. par l'appraition tardive d'elem. nouv. d. tiges et l. racines d. Dicot. These (Bordeaux(, Paris 1879. Russow, Z. Kenntn. d. Holzes. Insonderheit d. Koniferenholzes. Bot. Cbl. 1883, Bd. XIII, p. 134. Prael. Vergl. Untersuch. ub. Schutz- u. Kerhnholz d. Laubb. Pringsheim's Jahrb. f. Wiss. bot. 1888, Bd. XIX, p. 1. (compare Ber. d. D. Bot. Ges., 1887, Bd. V, p. 417). Williamson, On some anamalous cells developed within the interior of the vascular and cellular tissues. etc. Ann. of Bot. 1888, Bd.I.p. 315. Conwentz, Ueber Th. u. thyllenahnl. Bildungen, vornehmlich im Holz d. Bern-Baume. Ber. d. D. Bot. Ges. 1889, Bd. VII, p. 39). Tubeuf, Ueb. normale u. pathogene Kernbildung d. Holzpfl. u. s. w. Zeitschr. ges. Forst. u. Jagdw. 1899 Bd. XXI, p. 385, Raatz. Uber Thyllenbild. in d. Tracheiden der Koniferenholzer. Berichte d. D. Bot. Ges. 1892, Bd. X, p. 183 (compare Conwentz, ibid., p. 218). Maule Der Faserverlauf im Wundholz. Bibl. Bot. 1895, Bd. XXXIII, p. 5,6.Anteil d. sekund Holzes d. dikotyl Gewachse an d. Saftleitang u.s.w. Wieler, Ueber d. Anteil d. Pringsheim's Jahrb.f.wiss.Bot. 1888, Bd. XIX,p.82.Ueb.d. Vorkommen v.Verstopfungen in d Gefassen monokot. u. dikot. Pfl.Meded.Proefsta. Mid-Java,1892.

Elaegnus
Euphorbia
Fagus
Ficus
Fraxinus
Gleditschia (Tison)
Hamamelis (Tison)
Hedera.
Hedychium
Heliconia
Humulus (Tubeuf)
Inula
Jatropha
Juglans
Koelreuteria
Latania
Laurus
Ligustrum
Loranthus
Loxopterygium
Maclura
Mansoa
Maranta
Micania
Morus
Musa
Ochroma
Olea
Ostrya
Passiflora
Paulownia
Perilla
Pharbitis
Philodendron
Phyllanthsu
Picea (Raatz)
Pinus (Raatz)
Piratinera
Pistacia
Plantageo
Platanus
Populus
Portulaca
Prunus (Wieler)
Pterocarya
Quercus
Rhus
Ricinus
Robina
Rosa (Maule)
Rubia
Rumex (Dutailly)
Salix
Sambucus
Santalum
Schinus
Sideroxylum
Solanum
Sparmannia
Stigmatophyllum
Strelitzia
Taraxacum
Thunbergia
Ulnus
Urtica
Xanthoxylon (Tison)
Vitis.

(104) So far as I known only Cyathea insignis may be considered as a representative of vascular cryptogams, in which according to Conwentz (loc. cit. p. 36), tyloses appear in the old petioles.

Two more important points are to be settled - the question as to the etiology of tyloses in the ducts and the question as to their physiological significance.

It has not yet been made sufficiently clear, under what conditions tyloses are produced. Beyond doubt, the parenchyma cells are stimulated to tylose formation through injury to the branches, roots, etc. Tylose formation appears as well in artifical pruning etc., as in the "physiological " injury, which defoliation brings with it; in Robinia only a few hours suffice to bring about the formation of tyloses after injury (according to Wieler).[1] We may therefore consider tyloses as callus-hypertrophies of the bark and other tissues. Like these and other hypertrophies tyloses also, as I have convinced myself by experiments with Platanus cuttings, are furthered in their developement by the action of air rich in moisture.

On the other hand, it is well known that the formation of tyloses may occur in very many plants, even without previous injury. In the heart-wood and in ageing sap-wood the ducts are filled with them. The question must remain undecided whether the in heart-wood, etc., similar factors act upon the parenchyma cells, as when branches are cut off, or in any kind of injury, or whether other conditions than these, effective after injury, can cause the formation of tyloses. The tyloses, independent of the wound stimulus, appear, however, not only in ageing parts of the trunk, but also in organs still very young; for example, in the Cucurbitaceae. The conditions which cause tylose formation in ageing organs seem therefore to be fulfilled occasionally in young ones also.

There are still other statements, according to which attacks by parasites exert an influence on the tylose formation. Tylose formation is said to appear after infection by fungi.[2]

In order to be able to explain uniformly, the production of tyloses in wound-wood and in heart-wood, Bohm assumed that the filling of the ducts with air, under the usual pressure, is the cause of tylose formation. Molisch (loc. cit. p. 295) has criticised this assumption; "In an injured branch, tyloses are formed bery abundantly perhaps 1/4 to 1 cm. below the wound, somewhat farther down markedly less frequently, until finally 2 to
(105) 3 cm. deeper they do not appear at all. If the sus-

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1. Wiler, Ueb. d. Anteil d. sekund. Holzes der dikotyl. Gew. an d. Saftleitung, etc. loc. cit. Fort the formation of tyloses after the falling of the leaves, see Staby Ueb. d. Verschl. d. Blattnarben nach Abfall d. Bl. Flora, 1883, Bd. LXIX, p. 113. von Tieghem and Guignard, Observat. s. l. mecanisme de la chute d. feuilles. Bull. Soc. Bot. France 1882, T. XXIX, p. 312. Tison, loc. cit. Therein also further bibl. Weber (Ueb. d. Einfl. höh. Temperat. auf d. Fahigkeit d. Holzes, den transpirationsstrom zu leiten. Ber. d. D. Bot. Ges. 1885, Bd. III, p. 345) obtained tyloses in the vicinity of pieces of branches which had been killed by heat.

2. Compare for instance, Mangin, Sur la maladie du Rouge d. l. pepinieres etc. C. R. Acad. Sc. Paris, 1894, T. CXIX p. 753 (Beob. an Ulnus and Ailanthus nach Infection durch Nectria cinnabarina). Prillieux and Delacroix. La gomose bacillaire, maladie des vignes. ANN. Inst. Nat. Agron. 1895, T. XIV.

pension of the negative air pressure in the ducts were the only cause of tylose formation, then, considering the well-known fact that the ducts usually stand in open continuity for far longer stretches,- often several meters long,- this would have to hold good for much deeper distances."

The question as to the function of the tyloses in the ducts causes great difficulty. The nature of the tyloses described above make it certain that they influence the functioning capacity of the ducts of which they have possession. Tyloses will stop up the water conduits by the close filling which they produce in the ducts and make them incapable of functioning. It seems doubtful, however, whether in this effect of tyloses, we may look for their significance from the view of physiological anatomy:- for some cases indeed it seems improbable. That tyloses are beneficial on the surface of wounds as obstructive precautions, may indeed be obvious, but it is inconcievable why an obstruction of the conduits should also be advantageous; at times in uninjured parts;- even in very young sections of shoots. Besides this, cases are not lacking in which tyloses remain much too small to make a perfect stoppage. For these reasons, Haberlandt[1] assumes that "the tyloses in some way interfere with the process of transporting materials, since they enlarge the contact surface of the parenchyma cells and ducts. Thus, for example, they could accelerate the compression of hemorrhage in the ducts, could force sugar into these ducts, or conversely like haustoria, which they resemble, could draw out from the transpiratory current certain substances dissolved in it. The circumstances that, according to Reess, the formation of tyloses often continues a long time in ducts several years old, seems to favor a function of this kind, it appears as if the old tyloses, having grown incapable of functioning, are replaced by new ones." Of course, for the present, this is all supposition.

Thus, the search for a physiological significance of the tyloses has not yet led to any satisfactory results. Perhaps the assumption brings us nearest to the truth, which suggests that many of these, like the hypertrophies already described, do nothing for the well-being of the whole organism but are to be considered as pathological formations in the sense discussed at the beginning of this book.

2. The secretion glands and the rosin canals, like the lumina of the ducts and tracheids may be filled up by tyloses through the outgrowth of adjacent living parenchyma cells. Among the cryptogams (Lycopodium), gymnosperms (Zamia, Pinus, Larix, etc.), and various kinds of angiosperms (Rhus, Hyper-

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1. Physiol. Pflanzenatomie, 2. Aufl., 1896, p. 283.

(106) icum, the mucus tubes of Anthurium, etc.), large numbers of cases of this sort are well known[1]. Tyloses of the secretory-glands, like those of the ducts, arise on the one hand after injury (as, for example, according to Tison, in autumnal defoliation), on the other hand as "phenomena of senility" without previous injury. But it would be impossible to say what factorys incite their formation, and whether they have any significance whatever for the life-activity of the organism as a whole.

3. Finally, those tyloses remain still to be considered, which grow into the air chambers of the stomata and fill them partially or entirely. Hypertrophies of this kind have long been known in many plants; either the epidermal cells lying adjacent to the guard cells, grow out on the inside into large bags, as Haberlandt[2] affirms for *Tradescantia viridis*, (compare fig. 33) or the neighboring mesophyll cells are distended and fill out the empty space. (fig. 34) The second type is more frequent. Schwendener observed the same in *Prunus Laurocerasus and Camellia japonica*, Molisch, in *Tradescantia guianensis, T. zebrina and T. pilosa*, and in *Begonia gunnerifolia, Haberlandt in Pilea elegans* (fig. 34) Mobius, in *Ficus nerifolia*, etc.[3] The intercellular spaces lying below the water clefts show at times a very similar filling out. (Tropaeolum Lobbianum, Cephalotus follicularis[4].) Occasionally the walls of the tyloses are greatly thickened on the side turned toward the guard cells. (Ficus, Pilea, fig. 34.)

It has not yet been observed whether tyloses are produced in the inner cavities of stomata after injury, but
(107) it may be possible to prove this by future investigations. They are produced chiefly on ageing organs, further, according to Haberlandt, on such as suffer from lack of water. A

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1. Unger Anat. u. Phys. d. Pfl., Pest 1855, p. 213. Hegelmaier and Pfeffer im Tagebl. d. Naturf.-Vers. Leipsig, 1872 p. 144, 145. Mavr, Ueb. d. Verteil. d. Harzes in uns. wichtigsten Nadelholzbaumen. Flora, 1883, Bd. LXVI, p. 221. Ensteh. u. Verteil. d. Sekretionsorg. d. Fichte u. Larche. Bot. Cbl., 1884, Bd. XX, p. 278. Trecul, s. l. cellules qui existent a l'inter. d. canaux du suc propre du Brucea ferruginea. C. R. Acad. Sc. Paris, 1887, T. CIV, p.1223. Tschirch, Angew, Pfl.-Anat., 1889, Bd. I, fig. 565. Conwentz, loc. cit. Mobius, Japanische Lackbaum, Rhus vernicifera. Abh. Senckenb. Naturf. Ges. 1899, Bd. XX, p. 201. Costerus, Les petits point fonces d. feuilles des Connarus. Ann. J. Bot. Buitenzorg. 1899, Suppl. II, p. 109.

2. Ueb. d. Bezieh. zw. Funktion u. Lage des Zellkerns bei d. Pf l. Jena 1887.

3. Schwendener, Bau und Meckanik d. Spaltoffn. 1881.Ges. Abh. 1898, Bd.I,p. 62. Haberlandt, Physiol. Pflanzenanatomie p. 400. Molisch loc. cit. Mobius, Beitr. z. Anat. d. Ficus-Blatter. Ber. Senckenberg. Naturf. Ges. 1887, p. 117.

4. De Bary, Vergl. Anat. d. Veget.-Org., 1877, p. 55, Göbel, Pflanzenbiol. Schild., 1891, 6d, II, p. 114.

thorough experimental investigation of the question, whether in such cases too great loss of water by transpiration actually incites hypertrophic growth, would be especially interesting since the only cases yet known are those in which abnormally large cells are formed as a result of too slight transpiration. The question whether tyloses of the air chambers are able to decrease the water transpiration of the leaves etc., in a way "expedient" for the organism, needs further investigation. In many cases the surface transpiring moisture might rather be increased by the abnormal mal growth of the mesophyll cells.

6. GALL HYPERTROPHIES

Those hypertrophies, which we will term gall-hypertrophies, have primarily a common etiological characteristic-gall-hypertrophies are those which are produced by the effect of a poison given out by a foreign animal or vegetable organism.

The abnormal tissue products, histologically most diverse, produced by the influence of foreign organisms, are differentiated from the corresponding normal tissues less by the size of their cells than by their number and their peculiar tissue differentiation. We will have to consider these supplementarily when discussing hyperplastic tissue structures . (Chap. V). I will defer until then a few general notes concerning galls, which are true also for the forms produced only by a cell growth. A complete, sharp line cannot be drawn in detail between hypertrophie and hyperplastic abnormal tissues even in those produced under the influence of parasitic organisms. Netherless I consider that the difference emphasized here is a suitable foundation for the division and that it makes possible the drawing up of groups and sub-groups, which may be termed "natural" ones on account of their correspondence etiologically and histologically.

In deciding the individual cases, the same questions are to be discussed as in the earlier groups;- questions as to the form of the hypertrophied cells and their internal structure. It must be shown that, in contrast to many other hypertrophies, the formation of those induced by foreign organisms is connected with an abundant supply of nutritive materials, with an "over-nutrition" which finds its obvious expression in an enormous accummulation of albumen, starch or the like.

Gall-hypertrophies occur extraordinarily often in the epidermal and fundamental tissues, in various plants and under the influence of the various animal and vegetable parasites.

a. Epidermis.

(108) In the next chapter it will be shown repeatedly that the epidermal cells in general participate only moderately in hyperplastic tissue formations; their "tendency" to cell division is slight. In hypertrophies, however, the epidermal cells play an important part. They are stimulated to growth by different kinds of parasites and furnish products of often astounding size and surprising diversity.

SYNCHYTRIUM GALLS

The galls of the Synchytria (Chytridiaceae) furnish instructive examples which may be cited first of all because of their simplicity. The course of development of these fungi, parasitic on different phanerogams, and their relations to the host plant are extraordinarily simple in as much as the whole life of one generation is enacted in one cell of the host plant. The swarm spores of the Synchytria penetrate into the epidermal cells of the parts of the plants above ground and incite the infected cells to active growth. Figure 35a shows the simplest case: the cells attacked by the fungus (Synchytrium Drabae Lüdi) have been enlarged, the form of the hypertrophied cells, however, not varying essentially from the normal . If the growth of the infected epidermal cells becomes greater, they push the mesophyll aside and grow into it as spherical or egg-shaped pouches,- often extending as far as the opposite epidermis,- or they swell out towards the outside and produce small hairs, as in the gall-product of Synchytrium Myosotidis shown in fig. 35b.[1] In the case of other Synchytria the nutritive cells assume still more complicated forms.

Besides the nutritive cell, in which the parasite remains the neighboring cells of the epidermis can be incited to abnormal growth, in which they do not change their form essentially. (Compare fig. 36a.) Finally, if cell division takes place near the nutritive cell, more or less extensive,
(109) often round warts, or warts with stalks, are produced, in whose centre, or at whose apex the nutritive cell may be found. (Fig. 36b). In the production of such multicellular galls, therefore, hyperplastic tissue-changes are also involved.

It is not yet sufficiently clear, what factors determine whether only the nutritive cell of the parasite hypertrophies, or other cells undergo an abnormal growth and division. This much is certain, that the nature of the parasites and the specific character of the host plants alone do not determine it, that therefore, the form of the galls cannot be ascribed throughout and unreservedly to the systematic characteristics of the different Synchytrium species. Ludi especially has referred to the change of the gall-form in the species named:- "Usually when the warts are close together, Synchytrium Drabae showed only those whose resting spores lie in more or less distended epidermal cells, and which have no further influence on the neighboring cells,- therefore, simple warts. Not infrequently and usually where there is more space at the disposal of the nutritive cell in its development, where therefore the warts are not so close together, the nutritive cell is distended

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1. Schröter, Die Pflanzenparasiten aus d. Gattung Synchytrium. Cohn's Beitr. z. Biol. d. Pfl. 1875, Bd. I, 1, p. 1.

towards the inside and displaces its neighbors. The wart can then be termed "half-composite". Finally, however, it may happen- and this is found to take place in all peduncles,- that a one or more layered, cup-like covering grows about the nutritive cell, as in the case of Synchytrium Mercuriales. It is there designated as a composite wart.[1] In Lüdi's contributions are found also references to those of earlier authors upon this qquestion.

(110)

The fact that after infection with Synchtria and during the abnormal growth of the "nutritive cells", appreciable amounts of nutritive stuffs may indeed be brought to them, as stated above under gall hypertrophies in general, is proved first and foremost by the growth and increase of the parasite. No other means of nutrition are at its disposal than these contained in its nutritive cells In vigorous consumption, however, there does not occur any striking accumulation of proteins, which is characteristic of many other hypertrophies. The formation of red coloring matter has been observed repeatedly in infected cells.

ERINEUM- STRUCTURES

As the second group of the gall-hypertrophies of the epidermis, there follows that of Erineum-structures, which surpass in diversity of form all other hypertrophies known in the plant kingdom.

In the accepted text books of plant pathology all those mite-galls are summarized as felt-galls or Erineum-structures, which appear to the naked eye as "felt-like coatings" of the infected plant organ. This limitation may suffice for the needs of the practical worker, but for our purpose a sharper formulation might be advisable. In cross-sections of the diseased leaf, etc. it is shown, that the felt-like covering has been produced only by the outgrowth (hypertrophy) of epidermal cells (compare fig.38), or that besides the hairs, multicellular cones and ridges have been produced by the excrescence of the fundamental tissue. Felt-galls of the second kind will be mentioned in the chapter on hyperplasia. In the present chapter, we are concerned only with the first named case. As Erineum-structures we will consider in the following only those variations from the normal which are caused by mites, and which like many Synchytrium galls, are characterized by hair-like hypertrophy of the epidermal cells.[2] The knowledge of the Erinea

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1. Lüdi, loc. cit. p. 8.

2. I consider it expedient to retain the old designation "Erineum", in spite of the change in meaning of the word since Persoon. (see below). On the other hand, it appears to me inexpedient, at the least very unnecessary, to provide the newly found Erineum structures (from the standpoint) of the binominal method of nomenclature) with a particular "species" name.

dates back to Malpighi[1] who observed on grape leaves the white coat of hairs caused by mites.[2] This formation was not investigated more closely until the end of the 18th century, Persoon (1798) considered the abnormal hairs to be fungi, which he united into a new genus "Erineum".[3] Link
(111) and Fries[4] differentiated several genera, according to the form of the hairs. Unger[5], corrected their error and ascertained that the threads described by the authors named were not fungi, but hypertrophied epidermal cells. The next step forward was brought about by the knowledge that the described hypertrophies were caused by mites. Fèe was the first to discover them among the Erineum hairs[6], and to recognize them correctly as the cause of mal-formation. The development and life-history of the mites have been determined since then by the numerous investigations of Siebold,

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1. Anatome Plantarum, London, 1675-1679.

2. The "Erineum populinum", which Malpighi at any rate knew, is produced by tissue outgrowth, not by hypertrophy of the epidermal cells. Concerning the galls described by Malpighi, compare Massalongo, Le galle nell, Anatome Pl. di. M. Malpighi Malpighia, 1898, Vol. XII, p. 10, and v. Schlechtendal, Melpighi's Abhandl. de variis plantarum tumoribus et excrescenciis. Bot. Zeitg., 1866, Bd. XXIV, p. 217.

3. Persoon, Tentamen dispos. method. fungorum, 1798, p.43.

4. Link (Berl. Mag. Naturf. Fr., 1809, p. 21) distinguished between Erineum Pers. and Rubigo n. sp. Fries, (Observ. mycol. 1815, T. I, P. 217, Syst. mycol. 1829, T. III, p. 520) distinguished three general, Taphria, Erineum, and Phyllerium, which he united into Phylleriaceae. Persoon himself later (Mycol. europ., T, II, p. 2) named Phyllerium, Grumaria (Rubigo Lk.) and Taphria as subdivisions of his genus Erineum. Schlechtendal (Denkschr. Bot. Ges. Regensburg, 1822, p. 73) and Kunze, (Mycol. Hefte II, Leipzig, 1823, p. 133) furnished further investigations from the same standpoint as that of the above named authors.

5. Die Exantheme der Pfl. und einige mit diesen verwandte Krankheiten der Gewächse pathogenetisch und nosographisch dargestellt. Wien 1833, p. 376. Meyen (Pflanzenpathologie, 1841, p. 242.) later expressed himself as did Unger, concerning the nature of Erineum.

6. Fee, Men. s. l. groupe des Phylleriacees. Paris et Strasbourg, 1834.

Landois, Thomas, Brioski, Frank, Appel and others.[1] The studies of Nalepa threw light primarily on the diverse forms of the parasites.[2]

Erineum hairs always form more or less thick turf-like groups for which there is no definite external form or definite size-proportions.

It is common for all Erineum structures that the outer walls of the epidermal cells either take part entirely in the growth of these cells or predominantly. Thus it is evident that the hypertrophied cell cannot display an enlarged reproduction of the normal epidermal cell, but a change of its cell proportions must be associated with the increase in its volumme.

In the simplest case, short papillae are produced by the "out-pushing" of the epidermal cells. If the growth of these cells continues, sac-like hairs are produced; slender, cylindrical forms with rounded tips, or club-like, distended ones with slender bosses and spherical or mushroom-like heads.

(112) Erineum galls with papillae-like elements are rare. Of course the sac-like hypertrophied cells undergo a papillae-like first stage. One may even see at times on the edge of the Erineum turf that the growth of the individual elements stops permanently in the papillae-stage. Only rarely is the matured turf composed throughout of papillae-like elements. An example is pictured in fig. 37. A piece of the blade of Stipa pennata is illustrated; at a the epidermal cells have been incited to hypertrophy by Phytoptus mites

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1. Siebold, Ber. Schles. Ges. Vaterland. Kulture, Entomolog, Sektion, 1850, p. 88. Landois, Eine Milbe (Phytoptus Vitis Land.) als Ursache des Traubenmisswachses. Ztsch. f. wiss. Zool, 1864, Bd. XIV, p. 363. Thomas, Fr. as the most important of his works should be mentioned-Ueber Phytoptus Duj. u eine grossere Anzahl neuer od. wenig gekannter Missbildungen u. s. f. Ztsch. f. d. ges. Naturwiss., 1869, Bd. XXXIII, p. 314. Zur Entstehung d. Milbengallen u. verwandter Pflanzenauswuchse, Bot. Zeitg., 1872, Bd. XXX, p. 281. Entwickelungsgeschichte zweier Phytoptusgallen an Prunus. Ztsch. f. d. ges . Naturwiss., 1872, Bd. XXXIX, p. 193, Beitre. z. Kenntn. der Milbengallen u. Gallenmilben. Ibid. 1873, Bd. XLII, p. 513. Aeltere u. neue Beob. ub. Phytoptocedidien. Ibid., 1877, Bd. XLIX, p. 329. Briosi, Sulia Phytoptosi della vite, N. Giorn. Bot. Ital. 1877, Vol. IX, p. 23. Compare Just's Jahresber., 1876, Bd. V, p. 1234. Frank krankh. d. Pfl., 1, Aufl. 1880, p. 671, 2. Aufl., 1896, Bd. III, p. 40ff. Appel, Ueber Phyto- und Zoomorphosen, Konigsberg, 1899, p. 41.

2. Sitzungsber. Akad. Wiss. Wien, math-naturw. Kl. 1889, Bd. XCVIII, Abt. 1, p. 112, 1890, Bd. XCIX, Abt. 1, p. 40 and later. Numerous supplements have appeared in place mentioned. Of the older zoological literature, I will name only the works of Dujardin (Ann. Sc. Nat. 1851,p.166) who founded the genus Phytoptus, and Pagenstecher (Ueb. Milben, bes. die Gattung Phytoptus. Verh. naturhist-mediz.Ver. Heidelberg,Bd. I,p. 46, Ueb. Phyt. Tiliarum, Ibid. Bd. III, p. 153).

(Tarsonemus) and have grown out to short, broad papillae with a granular outer surface[1]. Tarsonemus induces similar papillae on other Gramineae also (Stipa capillate, Triticum repens).

In the majority of cases, the Erineum turf consists of slender, cylindrical hairs of equal thickness and with rounded tips. In the leaves of Alnus, Tilia, Fagus, and other trees, the turfs occur on the upper or under side of the leaves, more rarely on corresponding areas of both leaf-surfaces (Compare fig. 38). They form extraordinarily thickfelts, since all or nearly all the epidermal cells on the infected place in the leaf hypertrophy as is shown in the illustration.

The non-cylindrical hairs, occurring on the leaves of Prunus Padus, Betula, Acer and others, have different forms in the different Erineum-galls. Either hairs with slender bases are found, which grow broader toward the tip and end with a round tip, or those with a sharply set-off, ball-like or roller-like head, or with a flat and mushroom-like one (Compare fig. 39), or they are depressed on the top, thereby becoming cap-
(113) like. If a tendency towards branching shows itself, lobated forms are produced (Fig. 44a). I observed unusual hair forms in the case of an Erineum of Alnus latifolia, which produced a powdery coating on the underside of the leaf. The hairs, by their ramification, had assumed a racemose form and the greatest variety was visible among them. A few hairs of this Erineum are shown in Fig. 40. In contract to the Erineum galls with slender, cylindrical hairs, only isolated epidermal cells have been transformed hypertrophically in those forms which have spherical or mushroom-like elements, as shown by Frank, loc. cit. (fig. 39). When the hairs are close together, their heads may often touch one another, be flattened out in one another, or even dovetail together with their short processes.

For the histology of the single Erineum cells,- as in the case of other gall-hypertrophies,- the abundant supply of
(114) nutritive substances is important, which is connected with the growth of the infected cells. The abundance of nutrition is demonstrated by the growth in thickness of the walls and especially by the storing up of proteins, starch and fatty oil in the interior of the hair cells.

The thickening of the wall is less conspicuous in the simple cylindrical forms than in those distended like clubs. Especially the parts of the wall toward the outer side are often very thick. Thickened and pitted also are the side and inner walls of the epidermal cells which have grown out to Erineum sacs, but are still united with the tissue of the epidermis. Similar changes occur at times in places where the Erineum hairs touch one another. According to Frank the slender hairs of the linden Erineum ("Erineum tiliae") can coalesce at the places of contact and form corresponding pits, just as do the tyloses which touch each other inside of the lumen of a duct (p. 100). In the case of club-like hairs, the heads, provided with short outgrowths, sometimes coalesce and furnish a kind of pseudo-parenchymatic tissue; Frank observed pit-like thin places in the membranes of the contact-surfaces.

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[1] Massalongo, Intorno all' acarocecidio della Stipa pennata L., causato dal Tarsonemus Canestrinii, N. Giorn. Bot. Ital., 1897, N. S. Vol. IV, p. 103.

The content of the Erineum hairs is extraordinarily rich in proteins, the vacuoles often contain red coloring matter (Tilia, Alnus, etc.). In Acer, Vitis and others only scanty amounts of chlorophyll are developed. The club-like hairs of a maple Erineum are very striking; in these an immense quantity of small starch grains are deposited, or smaller numbers of often very composite starch grains lie next one another like mosaic stones, filling the lumen of the cell. In other hairs of the same Erineum form, fatty oil is found instead of starch, which takes up part of the lumen of the bark in splen-
(115) did menisci or makes of the whole cell a filled oil-sac. Small starch grains and isolated oil drops occur frequently in the case of other Erineum forms. In those forms which I have investigated, a cell nucleus may be found in each hair, whose position, at least on the matured hairs, was not constant. I discovered the nuclei in club-like hairs sometimes in the stalk and sometimes in the head part.

Simultaneously with the change of the epidermal cells in the Erineum formation, the cell of the mesophyll also may sometimes be altered. They too gain at times in volume and not infrequently store up abundant starch. Generally their chlorophyll fades then. This co-operation of the mesophyll may be recognized macroscopically by the fact that the leaf occasionally appears to have been pushed out into cuculli on the places infected by the felt-gall. This warping always takes place in such a way that the Erineum turf lies on the concave side.[1] The tissue structure of the mesophyll on the infected places either remains normal (fig. 39) or arrested development, becomes evident in the processes of differentiation, the mesophyll then remaining homogenous. (Compare fig. 38).

Finally those gall forms should be mentioned briefly whose abnormal hairs are multicellular,[2] and those which are produced not by a new formation of hairs, but by hypertrophy of the normal trichome. Frank reports an "Erineum" of the last kind (loc. cit. p. 48) on Querous Aegilops. Similar formations occur elsewhere also.

Since Fee, we have become better informed concerning the etiology of the Erinea and know that their formation is to be traced back to the colonization of the plants by Phytoptus mites. Undoubtedly the stimulus, causing the abnormal growth of the epidermal cells, comes from a poison which the gall insects produce, concerning which nothing more is known. The substance given out by them seems often able to filtrate from one epidermal cell into another and thereby to stimulate those cells to hair formation which were not directly infected by the mites. If the mites affect the underside of a leaf, their virus can penetrate the whole thickness of the leaf and incite

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1. Compare also Meyen loc. cit. p. 243, who observed the embossment of the leaf and traced it back to enlargement of the single cells.

2. Neger, Ueb. einige durch Phytoptud hervorgerufene gallenartigen Bildungen. Verhandl. D. wissenschaftl. Vereins, Santiago 1895, Bd. III, p. 149.

the epidermal cells of the upper side also to the phenomena of growth here described. In this case corresponding areas on both sides of the colonized leaf are covered with Erineum turf (compare fig. 38). This action on the side of the leaf opposite to the surface primarily stimulated seems to be come evident especially abundantly on the leaves of Tilia, on which Frank had already found them. I observed the same phenomenon on the rough, upper leaves of the linden inflorescence. If we overlook the cases in which mesophyll cells also are incited to a weakened growth, we may assume that, in the formation of Erinea, those poisons are active, which incite only the epidermal cells to intensive growth[1].

Microchemic methods, making possible the proof of the spread of gall-poison in the plant body, are not at
(116) our disposal. We can recognize its diosmotic distribution only in its effects on the cells of the host plant. As noted above, the cylindrical hairs of the Erineum galls form thickly closed masses, sinch each single epidermal cell grows out into a hair. The assumption that the gall mites work so exactly and infect each cell separately is less probable than the one that the poisonous substance given out by them can diosmose from one cell to another. The hair formations on the side of the leaf not infected support this assumption. On the other hand the Erineum hairs are isolated if club-like or mushroom-like forms are involved. The possibility that for each individual hair an especial act of infection is necessary may be considered here, and also that the poisonous substance of the mites can not diosmose from one cell to another, or at least not in a sufficient amount. To my knowledge, there is no case known in which mushroom-like Erineum hairs had been formed on the side of the leaf not infected.

The question as to whether the epidermal cells of all parts of plants have this capacity for transformation may be answered only incompletely by a consideration of the materials offered in nature. Apparently all parts of the plants bearing Erinea, which are above ground, are capable of forming abnormal trichomes, so long as a living epidermis is present on them. To be sure most of the Erineum forms are found on leaves, but if the mites colonize on young petioles or parts of the stalks, the hypertrophies described are produced on these also. Most of the Erineum forms prefer the underside of the leaf, in the case of Fagus, Tilia, Prunus Padus and others, however, Erineum hairs occur on the upperside also. Cuboni[2] observed Erineum turf on bunches of grapes. Further, in many blossoms galls[3], trichomes often develop which comm-

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[1] Compare Küster, Cecidiol. Notizen I. Flora, 1902, Bd. XC, p. 67.

[2] Le stazioni speriment. agar. ital. Roma 1888, p. 524. Quoted from Frank, loc. cit. p. 49.

[3] Compare also Molliard, Cecidies florales. Ann. Sc. Nat. Bot. 8me ser., 1895, T. I., p. 67.

pletely resemble Erineum hairs (Compare also fig. 44). The fact that the forms of the Erineum hairs sometimes occur differently on different plant organs is worth notice and deserves further investigation. (Compare Frank, loc. cit. p.44).

Only experiments will give a reliable answer to the question whether the epidermis of all plants can be stimulated to the production of hairs by means of certain poisons. Discoveries in nature make it seem very probable primarily that the peculiarity of the epidermal cells now under discussion is at least very widely distributed, since Erineum galls are to be found upon representatives of the most varies plant families. The most numerous of the native Erineum galls are found upon deciduous trees;- among herbaceous plants the preference for the Rosaceae is strikingly noticeable.

Of the trees and shrubs bearing Eruneum, I will mention the following:

Acer	Quercus
Alnus	Rubus
Betula	Salix
(117) Crataegus	Sorbus
Evonymus	Tilia
Fagus	Viburnum
Prunus	Vitis
Pirus	

As examples of the herbaceous plants bearing Erineum:

Geranium	Poterium
Geum	Salvia
Mentha	Scutellaria
Potentilla	Veronica

More detailed summaries are to be found in the work of Unger[1]. Frank (loc. cit. p. 47), v. Schlechtendal[2], Neger (loc. cit.), Darboux and Houard[3] and others.

Finally brief mention must still be made of the hair-like outgrowths which are formed on different kinds of plants under the influence of Cyanophyceae. In the case of Axolia, Nostoc colonies always settle in the hollows at the base of the upper leaf lobes. A few of the epidermal cells covering the hollow, grow out into long hairs. In the leaf ears of the liberwort Blasia, colonized by Nostoc strings, may be foun d similar unicellular, much branched hairs. In the Anthocerotaceae also the wall cells of the mucus hollows inhabited by Nostoc grow

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[1] Loc. cit. p. 372. Therein also references to the older literature and some remarks on the plant geographical distribution of the Erineum galls.

[2] Loc. cit. Compare further: Uebersicht der bis. z. Z. bekannten mitteleuropaischen Phytoptocecidien und ihrer Litt. Zeitschr. f. Naturwis., 1882, Bd. LV, p. 480.

[3] Catalogue sustem. d. Zoocecidies le l'Europe et du bassin mediterraneen. Paris, 1907.

out into delicate, much branched and intertwined threads[1].

b. Ground-Tissue

The ground tissue of plants participates differently in the construction of the galls. In many-gall forms its elements are only enlarged, without division (Hypertrophy), in others very abundant cell divisions usually follows growth. We are concerned at present only with changes of the first kind.

It is easy to name a large number of fungus or insect galls in the production of which, for example, we find that the mesophyll of the leaves react by developing abnormally large cells but to the exclusion of all processes of division. In almost all cases, however, those galls are not involved here, the character of which depends upon the products of purely hypertrophic changes, but those in which the emission of cell division is to be observed only as indication of an incomplete development of the diseased form. Under "more favorable" external conditions gall hyperplasias instead of gall hypertrophies would have been produced by the same parasites[2].
(118) We will defer the consideration of these galls to the next chapter and limit ourselves in the present to those in which in accordance with the specific poisonous effects - only hypertrophic cell-changes are always concerned and only through these is produced the characteristic structural form of the gall-tissue. Phenomena of growth of the kind described can be caused by animal as well as by vegetable Symbionts.

As first instance, I will name those changes which are caused by Anabaena Cycadearum on the roots of the Cycadeae[3]. In a definite zone, the cells of the fundamental tissue grow out into sacs elongated like palisade cells, which leave free large intercellular spaces. The Anabaena threads remain in these. (Compare fig. 41).

Of the native Zoo-cecidia two fly-galls demonstrate excellently the process of growth here described.

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1 Leitgeb. Lebermoose. Bd. V, p. 16.

2 Similar considerations were given above (p. 97) in the discussion of callus hypertrophy.

3 Most important literature: Reinka, Morphol. Abhandle, p. 12, Zwei parasitische Algen. Bot. Zeitg. 1879, XXXVII, p. 472. Schneider, A. Mutualistic symbiosis of algae and bacteria with Cycas revoluta. Bot. Gaz., 1894, Vol. XIX, p. 25. Goebel, Organographie, 1901, p. 483. Life, Tuber-like rootlets of Cycas revoluta, Bot. Gaz. 1901, Vol. XXXI, p. 265. Pampaloni i. e. Nostoc punctiforme nei suoi rapporti coi tubercoli radicali delle Cicadee. N. Giorn Bot. Ital., 1901, N. S. Vol. VIII, p. 626.

Figure 42 shows part of a cross-section through the so-called window-gall of the maple[1]; a roundish spot of the leaf blade is appreciably swollen, since the cells of several layers of the mesophyll have been greatly enlarged and stretched at right angles to the upper surface of the leaf. The epidermis and usually also the cells of the uppermost palisade layer remain unchanged, the others have become thick, delicately walled sacs, rich in albumen, which usually do not show any chlorophyll content.

(119) More widely distributed than the window-gall of the maple is the reddish brown bladder gall occurring on the leaves of Viburnum Lantana which is produced by a Cecidomyine. So far as I know, this has not yet been clearly defined.[2] The leaf seems to be distended lense-like on the infected spot. A cross-section shows that the gall surrounds a cavity lined by greatly enlarged mesophyll cells and occupied by the larva. (Compare fig. 43). The changes in the mesophyll are about the same as those of the maple gall already described. The cells of all the mesophyll layers are soon elongated to about an equal extent. In other cases, the growth of the palisade cells or of the spongy parenchyma cells predominates. Thus rather irregular cell forms are often produced, as shown in the illustration. In all cases the chlorophyll content of the hypertrophied cells is extraordinarily scanty, or almost null, but their protein content is very large. Often abundant formation of anthocyan-in occurs which makes the galls visible even from a distance. Calcium oxalate glands are not infrequent in hypertrophied mesophyll.

Even the pith is able to develop gall-hypertrophies. In leaf blades of wheat, attacked by Chlorops taeniopus, the cells of the pith grow out into long thick villi "whose free ends are much twisted and bent and remind one, by their length, of the papillae of many stigmae". Cohn.[3]

The list of known gall-hypertrophies is not exhausted with those here described. An especial group is formed first of all by the giant cells - in which not only the protein content but even the number of nuclei increases dur-
(120) ing cell growth. Multi-nuclear elements are produced, which will be especially discussed in the next division, as transitions between hypertrophic and hyperplastic forms.

A number of other hypertrophies, produced under the influence of foreign organisms, will be mentioned in the following "appendix".

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1. Thomas, Fr. Fenstergalle des Bergahorns. Forstl. Naturw. Ztschr., 1895, Bd. III, p. 429.

2. V. Schlechtendal, Die Galbildungen (Zoo-cecidien) der deutschen Gefasspfl. Zwickau 1891, N. 1150.

3. Ueber die Bandfüssige Halmfliege (Chlorops taeniopus) Ber. Schles. Ges. Vaterl. Kultur. 1865, p. 77.

APPENDIX.

Purely formal correspondence with Erineum hairs already described neccesitates the mention at this point of a number of other hypertrophies and form-variations which are produced by the most varied causes, showing nevertheless a natural relationship. In the cases here summarized, in the first place, growing cells are concerned, which assume an abnormal form under the influence of abnormal life-conditions In the second place, cells with apical growth are constantly involved, root hairs, fungus hyphae, siphonae, pollensacs, and the like. In the third place, the same forms are repeated in all cases, even those which have been already described for the Erineum hairs. Further, we will be able to prove that the internal formation of the cell abnormally formed does not vary from the normal, if we do not include here the loss of cytoplasm, which cells often undergo in hypertrophy. Regular thickenings of the wall, formation of the cell-organs, such as chlorophyll grains, etc. are never found. Also, cell division never follows cell growth, nor is anything known of an abnormal nuclear increase. The changes are therefore only of a kataplastic nature. Formation of irregular cellulose accumulations is not infrequent.

The formal similarity of the roothairs to the cylindrical Erineum hairs is forthwith obvious; in both cases unicellular, almost always undivided, derivations of the epidermal cells are concerned. The differences between the two lie especially in the fact that the root hairs are always much more slender and often appreciably longer than the hairs of Erineum types. A comparison between the two is made especially important by the fact that under abnormal conditions roothairs can assume the forms described above as characteristic of definite felt galls. On their apices round or wart-like processes are produced, wavy rifts become visible and here and there even the beginnings of ramification.

Thorough investigations of this subject may be found in the work of Fr. Schwarz[1], who has furnished some information on the conditions under which abnormally formed roothairs may occur. Schwarz experimented with nutrient salt solutions of 1 to 10 per cent. "since only the osmotic effect produced by the salt is concerned here, even solutions of cooking salt, calcium or potassium nitrate may be used. The plants, however, are more easily injured by these than by a solution of nutrient substances." "A concentrated solution
(121) arrests the growth of the root hairs very markedly, however much it may favor their growth in thickness. If the hair should grow absolutely equally in thickness, a ball would necessarily be produced. This occurs only rarely and in very concentrated solutions (20 per cent.). On the contrary, the hairs often grow normally, later their diameter is increased and their form becomes distended, after this they again become more slender until another distension is formed. This

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1. Die Wurzelhaare d. Pfl. Tübinger Unters. Bd. I, Heft. 2, 1882, p. 135. Compare further, Wortmann, Beitr. z. Phys. d. Wachstums. Bot. Ztg., 1889, Bd. XLVII, p. 283 and Reinhardt, Das Wachstum der Pilzhyphen. Pringsheim's Jahrb. f. wiss. Bot., 1892, Bd. XXIIIm p. 557.

process may be repeated many successive times. (loc. cit., p. 183). The same changes in form may be obtained by transferring the root-hairs from moist air into water or into concentrated nutrient solutions. It is even possible by these methods to produce branched root-haits, occasionally mentioned in the literature on this subject.

The illustrations here shown should be convincing as to the similarity of the Erineum hairs to deformed root-hairs. In figure 44, the hairs of an Erineum of Acer campestre are shown side by side with club-like root-hairs, beginnings of branching showing on their distended heads. Further, in figure 45, three irregularly waved hairs from a blossom gall
(122) of Phyteuma are shown side by side with root-hairs, which Schwarz obtained by the methods desotibed above and which show very similar alternating constructions and distensions.

As Schwarz has shown, these abnormal root-hairs are produced after changes in the osmotic pressure of the cell, through retention in solutions which withdrew water from them, as well as by transferring from air to water. It does not seem possible that, besides the action of withdrawing water produced by the effective solutions, even specific poisonous action, proceeding from these solutions may influence the formation of irregularly deformed root-hairs. For comparison with those above described, root-hairs of Sinapis seedlings are also shown in figure 46, which were grown under treatment with very dilute sublimate solution. As may be seen the formal diversity is very great, even in adjacent hairs.

Hypertrophies occur further on rhizoids and root-hairs after infection by foreign organisms[1]. The abnormal progress of apical growth is connected supposedly with some effect on the turger in the cell. The same forms as in Erineum and root-hairs are found in a number of other tube-like cells, which are similarly enlarged by apical growth. In the following fungus hyphae the Siphoneae and pollen tubes may be briefly discussed. The deformations of the fungus hyphae are best known. They are extraordinatly abundant and in fact are present in any fungus-culture. The hyphae here and there form isolated boil-like spherical distensions or places with alternating narrow and wide lumina, corresponding to the

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[1] Examples in Magnus, Ueb. Chytridium tumefaciens n. sp. in d. Wurzelh. v. Ceranium flabelligerum u. acanthonotum u.s. w. Sitzungsber. Ges. Naturforsch. Fr. Berlin 1872, p. 87. Goebel, Morph. und biol. Studien. Ann. Jard. Buitenzorg, T. VII, p. 77. Boebel, Archegoniatenstudien, Flora, 1892, Bd. LXXVI, p. 106 (Beob. an Polypedium obliquatum u. Trichomanes rigidum). Marchand, S. une nostochinee parasite. Bull. Soc. Bot. France, 1879, Bd. XXVI, p. 336 (Observations on infected moss-rhizoids, especially Riccia). Nemec, Die Mykorrhiza einiger Lebermoose. Ber. d. D. Bot. Ges. 1899, Bd. XVII, p. 311 (Observations on Calypogeia). Borzi, Rhizomyea, nuovo Ficomicete, Messina 1884(swellings on the root-hairs of many monocotyledons and dicotyledons after infection with Rh. hypogaea).

above figures. Besides these, abnormal ramifications may occur.

123) The variations in form already described have been mentioned occasionally in works on mycology on account of their conspicuousness, but have only rarely beeen studied thoroughly. Reinhardt's reasearches on the conditions of their production should be considered first af all. Slight fluctuations in the concentration of the nutrient solution fluctuations of temperature, or action of poisonous substances cause these deformations. If the disturbances are of a permanent kind, the growing hypha tip is rounded up into a ball. "The growth in length stops with this spherical swelling, if resumed immediately, the outermost ball-calotte grows out agins to a tip, of larger or smaller diameter, according to whether a more luxuriant or a less extensive growth of the hypha ensues. Only in this way- the process being repeated successively- all the wavy profiles produced, while the completed condition shown in the growing hypha gives primarily the impression that the parts just back of the tip are swollen through turgor into cap-like forms." In the case of more extensive disturbance, the ball is flattened in front and the apical growth stops first, while the parts lying next to the sides grow still further and extend beyond the dormant tip like a circular wall, until the growth here also comes to a standstill. Often, after a few minutes, it is resumed not by the tip but by single points of this circular wall, which as sprouts, grow out apically into hyphae. (loc. cit., p. 496, 497)." I have given Reinhardt's descriptions in detail since they apply not only to the abnormal forms of hyphae, but also of other cells growing apically which are described here.

Growth in to a spherical form which Schwarz studied in root-hairs , occurs also in fungus hyphae and was observed by Klebs[1]. He sowed spores of Mucor racemosus in 3 per cent. citric acid solution. In this "spores of the fungus swell up to bladders, which may be said to be enormously larger in proportion to the original size of the spore (0.01) mm., since they can reach at times a diameter of 0.5 mm. These giant cells, however, are not always spherical, but often pear-shaped, or tubular,- at any rate very differently formed. When germinating, many spores first put out in different places short germination tubes, which then swell out as the spores themselves have done, so that whole groups of such connected bladders are produced. Such a giant cell has a thin cell-wall, a thin brownish cytoplasmic wall layer and very abundant cell-sap. Such cells themselves, further, put out pocketings, which at timese are cut off by a crosswall. After a little time the cells disintegrate." The tendency of mucor spores to swell greatly through the addition of citric acid had been previously observed by Brefeld.[2]

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1. Beding. der Fortpfl. b. einigen Algen u. Pilzen, 1896, p. 517.

2. Brefeld, Mucor racemosus u. Hefe. Flora, 1873, Bd. LVI, p. 385, 391.

By the action of foreign organisms deformations are also produced, just as in the rhizoids discussed above, whether the foreign living creatures remain outside of the hyphae cells or be colonized inside of them. Bladder-like
124) swellings and abnormal ramifications occur, for example, in the mycelium of Pezzia, through the action of an adjacent Aspergillus mycelium.[1] Intumescenses are produced also by the action of bacteria, etc. On account of their biological significance, the deformations found by Möller[2] in the fungi cultivated by tropical ants are especially interesting. The sterile mycelium of Rozites gongylophora, formed by the fungi gardens of the tugging ant (Atta) shows regular, ball-like swellings on the ends of the hyphae. United into thick groups they form the "kohl-rabi mounds which serve the ants for food. (Compare fig. 47). Essentially the same is shown by the fungi cultivated by the hair and hupp ants (Apterostigma and Cyphomyrmex) although their kohl-rabi mounds do not consist of such regularly formed hyphae-heads as do those of the Atta species. Möller's cultural experiments with Rosites gongylophora prove that the mycelium forms diverse swellings extraordinarily easily. He succeeded in producing the kohl-rabi mounds even on artificial nutrient media. It is not known what factors in the nest of the tugging ants are effective in causing the formation of the hyphae swellings. Finally, hypertrophies of the fungus hyphae should be considered, which are produced after colonization by parasites. They offer nothing essentially new for our anatomical considerations.[3]

Intumescences, cells with wavy outlines etc. occur also in the Siphoneae. Bryopsis and Udotea are faverable objects and may be cultivated easily often forming in cultures the deformations described. Thus they repeat ontogenetically all the details which Reinhardt had described for fungus hyphae (see above.).

(125) The fact that even in Siphoneae, intumescences can be produced by the action of foreign organisms is proved by

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1. Compare in detail the statements of Reinhardt, loc. cit. p. 502, 519.

2. Möller, A. Die Pilzgärten einiger südamerikanischer Ameisen. Jena, 1893. (Schimper's Bot. Mitt. aus dem Tropen, Heft 4.)

3. Examples in Cornu, Monogr. d. Saprolegniees. Ann. Sc. Nat. Bot. 1872, V[me], Serie., T. XV, p. 145. Cornu, Ber. d. D. Bot. Ges., 1889, p. 255. A. Fischer in Rabenhorst's Kryptogamenflora, 1892, Bd. I, 4, p. 34, 37, and other places. Zopf. Zur. Kenntnis d. Phycomyceten. Nova Acta Acad. Leop. 1884, Bd. XLVII, p. 168, 173, and other places. Raceborski, Pflanzenpathologisches aus Java, Ztschr. f. Pfl.-Krankh., 1898, Bd. VIII, p. 195. (The so-called conidia of Bactridium flavum are enormously enlarged cells of an unknown fungus host plant (Peziza?) in which lives an amoeba like parasite (Rozella? Woronina?).

the galls of different Vaucheria species, produced by a rotifer (Notommata Wernecjii)[1] In the tubes of this alga, terminal, or lateral, wart-like, pear-shaped, or spherical pouches occur, which bear several horn-like outgrowths. (Compare fig. 48). Each of the galls contains a mother-animal besides numerous eggs or young.

The pollen tubes which are capable of forming similar deformations should still be mentioned. In artificial cultures, intumescent forms may be obtained.[2]

As has been stated for root-hairs and the fungus hyphae, it may also be assumed that, in the Siphoneae and in pollen tubes, changes in turgor in the growing cell cause the variations in form here described.[3]

Finally, we must mention here the involution forms of bacteria, which Nägeli[4] first observed and named. By the action of unfavorable external conditions- for example. of an unfavorable nutrient medium, or too high temperature- many bacteria, especially the vinegar bacteria grow out into extensive diverse monstrosities. They become, long, often twisted filaments, bladder or spindle-like tubes, often having wavy outlines. Branched forms are also abundant, as in the case of deformed root-hairs, etc. The bacteriods of the nodules in the Leguminoseae illustrate such branched forms. In short, it is the same structural-repertoire, which

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1. Compare especially Rothert, Ueb. d. Gallen der Rotatorie Notommata Werneckii auf Vaucheria Walzi n. sp, Pringsheim's Jahrb., f. Wiss. Bot., 1896, Bd. XXIX, p. 525. Citation of literature also in Trotter, La Cecidiogenesi nelle Alghe. Nuova Notarisia serie XII, 1901.

2. Of the literature I will name Tomaschek, Eigentüml. Umbildung der Pollens. Bull. Soc. Imp. Nat. Moscou, 1871, T. II The same, Kulturen der Pollenschlauchzelle. Verhandl. d. Naturforsch. Ver. Brunn, 1872, Bd. XI, Halsted. Americ. Natur. 1886, Vol. XX, p. 261. Bot. Gaz. 1887, Vol. XII, p. 139, 285, Acqua, Contribuz. alla conosc. delle cellula veget. Malpighia 1891, Vol. V, p. 3.

3. Just as in the cell-sacs already described, thick and thin places alternate with each other, according to whether growth takes place chiefly in length or in thickness, in multicellular organs, thick and thin places can follow one another like a string of beads, if, in their development, the external conditions alternately arrest and favor growth in thickness. For roots resembling strings of beads, compare Sachs, Gesamm. Abhandl., Bd. II, p. 801.

4. Die nied. Pilze in ihren Bezieh. zu. den Infectionkrankh, 1877.

we see repeated everywhere.[1] The correspondence of degenerate bacteria with the cells of higher and lower plants described above should be demonstrated by figure 49, which gives involution-forms of Bacterium Pasteurianum, and by the illustrations given earlier. Involution-forms of the bacter-
(126) ia are characterized by their small cytoplasmic content. The deformed cells finally disintegrate through loss of power.

Monstrosities occur also in the case of other unicellular living creatures, when cultivated under abnormal life conditions. These are produced in the same way by abnormal increase in volume and processes of growth taking an abnormal course. Algae, fungus spores and vegetative fungus cells also form such "involution-forms". Algae cells, conspicuous for irregularity of form and tendency to form branches, were observed for example in Stichococcus by Af. Klercker, Matruchot and Molliard, by Kruger in Chlorothecium saccharophilum Beverinck in Scendesmus acutus, etc.[2] I may name here also the giant algae cells, which are produced by the action of

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1. Literature on involution-forms collected, for instance in A. Fischer. (Vorlesungen ub. Bakterian, 1897, p. 162). Compare further for the action of nutrient substratum, Matzuschita. Einwirk. d. Kochsalzgehaltes des Nährbodens auf die Wuchsform d. Mikroorganismen. Ztschr. f. Hyg. u. Infectionskrankh, 1900, Bd. XXXV, p. 495, of temperature, Hansen, Rech. s. l. bacteries acetifiantes, Travaux du labor de Carlsberg 1894, Vol. III. Michaelis, Beitr. z. Kenntn. d. thermophilen Bakt. Arch. f. Hyg. Bd. XXXVI, p. 285, of substances eliminated by foreign organisms Potts, Zur physiologie des Dictyostelium mucoroides. Flora, 1902, Bd. XC, p. 281.

2. Af. Klecker, Ueber zwei Wasserformen von Stichococcus, Flora, 1896, Bd. LXXXII, p. 90. Matruchot and Molliard, Variations de struct. d'une algue verte sous l'infl. du milieu nutritif. Rev. gen. Bot. 1902, T. XIV, p. 113. Kruger, W. Kurze Characteristik einiger nied. Organismen im Saftflusse d. Laubbaume. Hedwigia, 1894, Bd. XXXIII, p. 241. Beyerinck Kulturversuche mit Zoochlorellen, Lichenengonidien u. and. nied. Organismen. Bot. Zeitg. 1890, Bd. XLVII, p. 724. Compare also Richter, Ueb. d. Anpassung d. Susswasseralgen an Kochsalzlosungen. Flora, 1892, Bd. LXXV. p. 4. Lockwood, Formes anormales chez les Diatomees cultivees artificiellement. Arch. Micrographie, T. X. p. 5. Miquel. Rech. experim. s. la phys. morph. et pathol. des Diatommes. Ibid. p. 49. The latter obtained abnormal forms in older, exhauseted cultures, especially if they were contaminated by other algae (Scenedesmus and others). It must remain undecided, whether possibly the irregular, many armed forms described by Bohlin (Ueb. Schneealgen aus Pita-Lappmark, Bot. Cbl. 1895, Bd. LXIV, p. 42) as Cerasterias nivalis, the strikingly variable forms described by Schmidle (Ueb. drei Algengenera. Ber. d. D. Bot. Ges., 1901, Bd. XIX, p. 10) as Coccomyxa dispar and similar algae forms might also be included among the pathologically deformed ones.

fungus-hypjae in the formation of lichens.[1] Gamaleia[2], Matzuschita (loc. cit.) and others observed "involution-
(127) forms in *yeast*. Schostakowitsch[3] gathered sausage-like or lobated spores from *Mucor proliferus*.

The question whether the deformations here described are connected in all cases with an injury of the cells infected, i. e., in the organisms here concerned, -may not be decided definitely. In any case the injury is often only slight and is felt only temporarily. In many cases indeed root-hairs and fungus-hyphae continue their growth normally after the formation of some distended places, intumescences, In extreme cases the injury is unmistakable. In involution-forms of bacteria and in the deformations of Mucor mycelium described by Klebs, the cells gradually lose their cytoplasmic contents and literally grow until they die,- comparably to the cells of the hyperhydric tissue, discussed above. Thus in these too we may speak of a decided kataplastic hypertrophy.

7. Multinuclear Giant Cells.

Multinuclear cells have already been mentioned. If cells of Spirogyra filaments, or the like, continue their growth normally, if the nuclei divide regularly but for some reason the formation of cross-walls becomes impossible, it then results in multinuclear cells. (See above p. 69). In the following, cases are to be described, in which cells of any kind are stimulated to abnormal growth, and their nuclei to division, without the formation of cross-walls. We can designate cells of the latter kind as transitions between hypertrophies and hyperplasias. To this must be added the fact that many giant cells subsequently form septa, after repeated nuclear division, just as we could prove above for giant cells produced by a continuation of normal growth-activity. It must be added further that, simultaneously with the production of multinuclear giant cells, abnormal cell divisions take place in adjacent tissues, by which nuclear division and cross-wall formation are related to one

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1. Stahl, Beitr. z. Entwickelungsgesch. d. Flechten, 1877, Heft 2; Compare also Lagerheim, Ueb. eine durch d. Einwirkung v. Pilzhyphen entstehende Varietat. v. Stichococcus bacillaris Nag. Flora, 1888, Bd. LXXI, p. 61. Bonnier (Germination d. lichens s. l. protonemas d. mousses. Rev. gen. de Bot., 1889, T. I. p. 165), obtained irregular, swollen cell forms on the moss protonema plants colonized by fungi.

2. Quoted in Jahresber f. Tierchemie, Bd. XXVI, p. 923.

3. Einige Versuche üb. d. Abhängigkeit d. M. pr. v. d. auss. Beding. Flora, 1897, Bd. LXXXIV, p. 88.

(128) another[1] as usual. We will not discuss further the question as to whether giant cells are to be classed with hypertrophies or hyperplasias, but will speak of them here as a connecting link between the two.

Only those hypertrophies can become multi-nuclear giant cells, in which the increase in cell volume is not produced predominantly or exclusively by wall growth and absorption of water, but is connected with an abundant increase of the cytoplasmic content. In hypertrophies of the first kind; for instance, in bark excrescences, I know of only uni-cellular forms. It does not seem impossible that in these or similar hypertrophies, further investigations will be able to prove phenomena of degeneration and decay of the nucleus. However, increase of the nuclear substance and division of the nucleus in one of two known ways (karyokenesis and amitosis) will undoubtedly remain restricted to those hypertrophies, whose cytoplasm is abundantly increased. Accordingly, giant cells occur predominantly in galls. On the other hand, it is necessary to call attention again to many gall-hypertrophies in which in fact very abundant cytoplasmic increase occurs, but no nuclear division.

(129) Most frequently observed and most exactly investigated are the giant cells of the nematode galls (produced by Heterodera) occurring on very different host plants and showing everywhere a similar inner structure[2] (Coleus, Circaea, Plantago, Beta, Daucus, Cucumis, Saccharum).

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1. At the first glance, it may seem forced to discuss in two different places the abnormal multi-nuclear cells, which as is well known, are formed in animal and human bodies through different causes. In the cases gathered together in the first section (the simplest cases), the multi-nuclear condition of the cells is caused by the fact that growth and nuclear division are continued normally, the formation of cross-walls being omitted abnormally. As remarked above, it was possible to justify the conception that giant cells of this kind represent "arrested development", in which the process of cross-wall formation is completely or partially "arrested". In the other kind of giant cells, they have the character of unmistakable hypertrophies; the cell is incited to abnormal growth and the nuclei to division, without the simultaneous fulfilling of the conditions necessary for division of the cytoplasmic body and for the formation of cross-walls. This conception is possibly better suited to explain the processes enacted in the plant body, in the formation of giant cells, than is Ribbert's assumption that in the abnormally enlarging cells, "the injured protoplasm was unable to divide, while the nuclei had suffered less". (Lehrb. d. allgem. Pathologie u. d. allg. path. Anat., 1901, p. 198).

2. According to the statements of the following authors:- Treub, Quelqu. mots. s.l. effets du parasitisme de l'Heterodera javanica d.l. racimes de la canne a sucre. Ann. Jard. Buitenzorg. 1887, T. VI, p. 93. Vuillemin and Legrain, Symbiose de l'Heterodera radicicola avec l.pl. cultivees au Sahara. C.R. Acad. Sc. Paris 1894, T. CXVIII, p. 549. Molliard, Sur quelqu caracteres histolog. des cecidies prod. par l'Heterodera radicicola. Rev. gen. Bot. 1900, T. XII, p. 157. Tischler, Ueb. Heterodera-Gallen an d. Wurzeln. v. Circaea lutetiana L. Ber. d. D. Bot. Ges. 1901, Bd. XIX, p. 95.

According to Tischler's observations on the nematode galls of the roots of Circaea many cells of the pleroma are stimulated to abnormal growth. Large, irregularly formed giant cells rich in cytoplasm are produced, many of which remain uni-nuclear, the rest becoming multi-nuclear. Figure 50 shows a group of multi-nuclear giant cells from an older Circeae gall. The cytoplasm of the giant cells has begun to disappear. Figure 50 c. shows a single giant cell with numerous nuclei, 50 b. isolated nuclei in one phase of division (amitosis by "budding").

Multi-nuclear giant cells occur also in other kinds of galls. Toumey[1] found them in "crown-galls" and in root excreseences, which in America infect various woody growths, apple, pear, peach, cherry, plum, chestnut, poplar, blackberry, walnut, etc. According to his careful investigations the disease is produced by a slime-fungus (Dendrophagus globosus)[2]
(130) The infected tissues are stimulated to abundant cell division; thus producing the multinuclear giant cells. These, however, do not differ so noticeably from cells normally constructed, such as the giant cells of Heterodera galls. Giant cells are usually segmented subsequently by cross-walls, so that uni-nuclear cells are again produced, (compare fig. 51). Judging from Toumey's drawing, these differ but little from the normal ones. Figure 51 shows, side by side with cells still multi-nuclear, some which have been divided by segmentation into uni-nuclear elements. Subsequent formation of cross-walls is noted also by Vuillemin and Legrain for the giant cells of many Heterodera galls. (Loc. cit.)

Multi-nuclear giant cells have been found further in the galls of the blood louse and in mite galls.[3]

Giant cells very similar to those found in galls are produced also by experimental interference. Prilleux[4] produced multi-nuclear giant cells in seedlings, which were cultivated at an abnormally high temperature. The number of the nuclei, however, rarely exceeded three. They were often ir-

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1. An inquiry into the cause and nature of crown-gall. Arizona Exper. Sta., 1900, Bull. XXXIII, p. 51.

2. Compare also Müller-Thurgau. 2 Jahresber. Versuch-station Wädensweil.

3. Prillieux, Etude des alterations prod. dans le bois, du pommier par l. piqures du puceron langiere. Ann. Inst. Agron., 1877-1878, p. 39 (Bot. Cbl. Bd. I, p. 436). Prillieux might well have been the first to observe multinuclear giant cells in galls. Molliard, Hypertrophie pathol. des cellules veget. Rev. gen. Bot., 1897, T. IX, p. 33. Sur les modifications histol. prod. d. l. tiges par l'action des Phytoptus. C. R. Acac. Sc. Paris, 1899, T. CXXIX, p. 841.

4. Prillieux, Alterations prod. d. l. plantes par la cultures d. un sol surchauffe. ANN. Sc. Nat. Bot. 6me ser., 1880, T. X. p. 347.

regularly lobated and contained several nucleoli. Further Raciborski[1] produced the formation of multi-nuclear giant cells in Basidiobolus ranarum by cultivating the fungus at 30 degrees C., in 10 per cent. glycerine. At first cell division followed nuclear division. later the former was omitted and giant cells with from 2 to 20 nuclei were produced. (Compare fig. 52) . The last named cases make it evident at once that no sharp boundary may be drawn between the hypertrophies here named and those cited under 1.

(131) Aside from enrichment in cytoplasm, no further changes are enacted in general in cells enlarging abnormally. The walls of the multi-nuclear giant cells usually show no variation from the normal. In regard to the statements concerning thickening of the walls in Heterodera galls (Viullemiin and Legrain Loc. cit.) compare Tischler's reports (loc. cit., p. 105).

Tischler investigated multinuclear giant cells from the cytological side. Attention has been called already to "amitosis through budding" which he observed. Reference must be made to the original work, in regard to the chromatin structure of the nuclei, the "pseudo-nucleoli" etc. Amitotic nuclear division occurs also in the giant cells of the germinating seedlings studied by Prillieux. In these, those nuclei are noticeable, which often divide without any spearation of the individual pieces from one another: "Un tel noyau multiple et hypertrophie presente a peu pres l'aspect d' un petit corps pluricellulaire." Figure 53 illustrates a nucleus of this kind, in which seven pieces may be distinguished. Raciborski proved positibely that the nuclei of the cells which he studed are produced by karyokinesis.

Nypels[2] found in the stem of Ranunculus repens giant cells (multi-nuclear?) which exceeded the volume of normal cells by "une centaine de fois". Parasites do not seem to have taken part in their formation.

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1. Raciborski, Ueb. d. Einfl. äuss. Bedingungen auf die Wachstumsweise des Basidiobolus ranarum. Flora, 1896, Bd. LXXXII, p. 113.

2. Notes de pathologie veget. C. R. Soc. Bot. Belgique, 1897, T. XXXVI, p. 249.

HYPERPLASIA

With Virchow[1], we will term hyperplasia all abnormal quantitive increase, which is produced by cell-division.

A sharp, unbroken line may not be drawn between the formal spheres of hypertrophy and hyperplasia without dissolving many of the "natural" groups of abnormal tissue formations which we have already established. We thus term as "natural", those groups of which the members are identified as belonging together not on account of only one characteristic, but of several,- histologic, ontogenetic, etiologic. In order not to break up groups of this kind, we spoke in the previous chapter of some abnormal tissue formations, which are produced not only by cell growth, but also, under certain circumstances, by cell-division. Reference is made to the places here concerned (especially pp. 86-109). In the present chapter we will have to consider a thoroughly uniform material, since only forms of disease will be discussed in it, which are produced by abnormal cell-division.

In the phenomena termed hypertrophies, it was often left undecided whether they are produced by the supplying of nutritive substances and "over-nutrition", or were accompanied at least by processes of this kind and, not infrequently, it had to be stated as absolutely impossible that such processes could produce them. In hyperplasias, however, there is nothing against the assumption that the place of abnormal tissue formation is always the goal of an especial nutritive current; that therefore an abnormally abundant supplying of nutritive substances always precedes the process of abnormal cell-division[2]. Therefore the sap currents, lying at the base of hyperplastic processes, can correspond very well to the currents in the normally developing plant so far as their direction and strength is concerned. If,
(133) for example, the vessels are broken at any point of the plant body, it may be assumed that the normal continuance of the transfer of substances will result in an accumulation of material at the place of interruption. Just as we have previously traced metaplastic changes to such accumulations of food-stuffs (compare p. 59), we will try in the following pages, to explain hyperplastic processes also by a similar over-nutrition. From these cases those others differ but little in which, as a result of the breaking of the vessels or the non-use of material, a great quantity of food stuffs is brought to places, to which, under normal conditions, only moderate amounts would have flowed. Thus, by cutting back growing shoots, dormant axillary buds may be forced to break, indeed even the leaves already present may be stimulated to a more luxuriant growth. Sacks[3], having removed all sprouting points from Cucurbita plants, caused the embryonic root cells adjacent to each petiole to grow out into extensive tubers, even as large as walnuts. In cases of the latter kind, we will speak of "correlation-hyperplasia".

In other cases the abnormal accumulation of material which precedes hyperplastic changes in tissue may not be explained thus simply by an interruption of the normal nutritive streams, or by

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[1] Cellularpathologie, 1858, p. 58

[2] From a medical point of view, Cohnheim (Vorles. üb. allg. Path., 1882, Bd. I, p. 703) has referred especially to the connection between abnormal formation of tissue, and increase in supply of food stuff.

[3] Gesamm. Abhandl., Bd. II, p. 1172.

the non-use of their material. For example, in many gall-formations, extensive tissue excrescences are produced, into which astonishing quantities of food stuffs wander, without the existence of any previous injury to the plant body, even the very slightest one, which could have led to an abnormal accumulation of material. We must assume that, in cases of this kind, the production of definite currents of food stuffs in abnormal directions which are surprisingly large arises from the action of stimuli, noticeable in the infected cell of the host plant after infection by parasites and under the influence of some unknown poison given out by them.

Among vegetative hyperplasias a number of well-differentiated groups may also be distinguished according to their etiology. Many are produced by chemical stimulation, others arise after injury, etc. In many the proliferation of the tissue may be traced back to the clogging of normal currents of food stuffs, in others to an abnormal bringing in of food, resulting from a local non-use of building materials. In still others, we must assume the existence of special stimuli, which bring about an abnormal supply of food, thus making possible hyperplastic tissue-formations.

When considering etiological conditions, we generally find ourselves in a more favorable position than do human pathologists, to whom the cause of many new formations of tissue is still unknown.

The abnormal tissues even show a diversity among themselves which is not found in any of the chief groups previously discussed. The outer forms of the excrescences, as well as their life history and their histology offer a profusion of noteworthy differences, the study of which will be our task.

(134) It will suffice first of all to sketch hastily the most important points of view.

Abnormal new formations of tissue deform the plant organs either as localized, more or less sharply defined excrescences, as diversely formed protuberances, as loosely attached "gall apples", etc. or they change a whole organ im such a way during the formation of the abnormal swelling, that the organ itself is at the same time completely consumed and thus, morphologically as well as physiologically, completely gives up its peculiar character. Figures 54 and 55 demonstrate this for a few galls. In the piece of an elm branch shown in the first figure, the leaf at the left has been caused to form an enormous, pale green pouch by Schizoneura lanuginosa, but has not been taken up as a whole. The form of the leaf has been kept pretty well and a large part of it has not lost the possibility of performing its functions. The same holds good in the galls shown in figure 58 and in many others.

Figure 55 illustrates two different Cynipides galls, in which buds of the oak have assumed a striking conical form (Cynips polycera) or have been grown out into long spindle-like structures, (Cynips aries). The infected organs have thus lost their normal form and function.

While, in the cases shown in figures 54 and 55 and in numerous others, the new tissue formation assumes a definite, usually very elastic form and definite size proportions are regularly repeated in the same kind of galls, there are still other hyperplasias, in the development of which - speaking figuratively - nothing of this morphologic striving towards a goal can be recognized,- hyperplasias in which all specific formal character is lacking and whose period of growth has no definite limitation. Examples of this second case are furnished by wound-tissue, fungus-galls and others.

In studying the life-history of hyperplastic excrescences, the cell-division producing them will have to be tested first of
(135) all as to their direction. We will find extensive tissue excrescences, of which the cell walls show a perfectly regular arrangement. In others a definite orientation can be found only in the first cell-divisions. When considering galls, the difference between cell divisions parallel to the upper surface of the organ, bearing the gall, and those perpendicular to it will be proved worthy of attention.

Further the tissue material, from which hyperplastic excrescences come, needs more exact testing from various points of view. The excrescence may be traced either to meristematic tissue or to permanent tissue. In the first case the direction of the division, characteristic of the meristematic cell under normal conditions, must be compared with that recognizable in normal tissue formation.

If the tissue excrescence arises from an organ or part of an organ of which the tissues are already differentiated, the further question arises as to whether all the different kinds of tissues of a normal organ are equally adapted to the production of abnormal tissues masses. It will be possible to determine conformably in hyperplasias of different kinds that the cells of the different tissues possess different degrees of capacity for abnormal division; thus, for example, the epidermis remains considerably below the mesophyll and bark tissues in its productive power.

(136) Finally the histology of abnormal excrescences will have to be studied. One of our chief tasks therefore will be a comparison of structures of abnormal tissue with the normal ones of its ground tissue, i. e. if deformations of the whole organs are concerned, to compare the structure of the organs deformed hyperplastically with that of the corresponding normal ones.

In all cases when judging of any tissue excrescence whatever, we will have to determine first of all, whether the abnormal tissues resemble the normal, corresponding parts of the plant, or whether they differ from them in any way. This question is of fundamental significance for our anatomical considerations; indeed, we will divide all hyperplastic tissues into homooplastic and heteroplastic ones according to the answer found. We will speak of an homooplasm if the cells produced in a tissue excrescence resemble the cells underlying them or adjacent to them and of an heteroplasia if the abnormal excrescences are composed of cells differing from the corresponding normal ones.

Heteroplastic excrescences are of especial histological interest. As might have been expected from the beginning the differences between normal tissue and the abnormal derivations, deviating from it in structure, are very diverse. For example, there is often a striking difference in size between normal and abnormal cells. The difference in tissue-differentiation, however, is of greater importance. In very many cases the product of the heteroplastic tissue formation is but little differentiated. So far as the form of the separate cells and the differentiation of the different tissue layers is concerned, we meet here with primitive conditions similar to those found in hypoplasia; In other cases, extensive differentiation occurs in the tissue, which,- corresponding to the character of the heteroplasias,-

differ from the normal and often exceed them in complexity. Therefore, in all heteroplastic tissue formations, we will be obliged to prove what the nature of the difference is between normal and abnormal tissue differentiation. If less differentiated tissue is produced by abnormal cell-division we can, without regard to the abundant increase in cell numbers speak similarly of a degeneration in the tissue formation, as we did above (p. 87) of a degeneration of the cell, which was combined with great increase in volume. We will speak here too of Kataplasy and term Kataplasmas the products of kataplastic processes[1]. If, on the other hand, new kinds of differentiation processes make themselves felt in the formation of abnormal excrescences, which are not known in the life history of corresponding normal tissues, we will speak of prosoplasia and prosoplasmas. Further differences between kataplasmas and prosoplasmas will be discussed later.

Kataplasmas will be exclusively involved in most of the tissue forms, with which we shall be concerned when discussing heteroplastic tissue. It will be shown that prosoplastic tis-
(137) sue formations may only be found among galls, but not that, conversely, all galls belong by any means to prosoplasmas, just as this very extensive and varied group of abnormal tissue formations is proved to be a homogeneous group, only etiologically and not histologically.

As was done in the preceding chapters, we will here base the division of our material upon etiological and histological characteristics:

Group 1. Homoeoplasia. The abnormal tissue is composed of the same elements as the original one.
Group 2. Heteroplasia. The abnormal tissue is composed of other elements than is the original one. Those heteroplastic products come under consideration as the most important, which are produced after injury (callus-formations), and those, which are caused by parasites (gall-formations).

Before we pass to the detailed discussion of different hyperplastic tissues, we must emphasize the fact that division not infrequently takes place in plant cells, which we must term abnormal although no hyperplastic tissues whatever are produced by it. The variation from the normal may consist in the abnormal direction of the newly formed cross-walls, or in the formation of the new cross-wall at a "wrong place", so to speak, while keeping to the direction, so that the normal size proportions of the daughter cells are not produced. Of course, only those abnormal cell-divisions belong in hyperplasias, by which the cell-number produced, is abnormally large for the tissue or organ concerned. Since no opportunity will arise later for returning to abnormal processes of the first kind of cell-division, a few examples may be mentioned here.

Cell-division in abnormal directions may be studied especially easily in those organisms or organs, in the normal cell-division of which, one definite direction is constantly repeated. Raciborski[2] observed on Basidiobolus ranarum that, by increased concentration of the nutrient solution, the direction of the

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[1] In regard to Beneke's treatise by which the term Kataplasy was introduced, compare above p. 68, note 1.

[2] Raciborski, Ueb. d. Einfl. äuss. Beding. auf. d. Wachstumsweise des Basidiobolus ranarum. Flora, 1896, Bd. LXXXII, p. 113.

cross-walls is displaced more and more until it finally can occur at right angles to the normal direction. Schostakowitch[1] observed similar phenomena. He found that Dematium pullulans can be developed in the form of small tissue bodies by the action of a higher temperature. Figure 56 shows a thread of
(138) Hormidium nitens of which cells have been irregularly divided under the influence of Congo Red[2]. Kny's[3] investigations throw light upon the influence of mechanical pressure and strain on the direction of cell-walls.

Miehe[4] observed cross-walls which are not formed at the place where they would appear under normal conditions. As has been known since Strasburger, the mother-cells of the stomata in the leaves of many monocotyledons are produced on the apical end of the dividing epidermal cell. By different kinds of experimental interference Miehe has succeeded in reversing this "polarity" in such a way that the mother cells of the stomata are cut off on the basal end. Klebs (loc. cit) observed unequal cell-division in Oedogonium etc.

A. HOMÖOPLASTIC TISSUE

We will term homooplasia each abnormal tissue formation, which is produced by an increase of the normal elements. It should be noted here, that "homooplasia", in our sense of the word, is not present in every increase of the normal elements nor in every abnormal increase in volume of any organ whatever. Through the cutting back of growing shoots, it is possible in many plants to produce especially large leaves on the stump of the shoot. Luxuriant nutrition leads often to the same result, as demonstrated by the side leaves of many root sprouts which have developed similarly to foliage leaves. Further, side l leaves may be brought to abnormally luxurient development by the removal of the foliage leaves which belong there, as shown by Göbel. Now, since abnormally large leaves of this kind are composed of cells approximately as large as those in the small normal ones, the large organs must without question be produced by an overproduction of normal cells. It is clear, however, that abnormal formations of this kind can not be the object of our anatomical consideration, since, in the cases cited and in analogous ones, anatomical variations from the normal are not necessarily connected with the increase in volume. The abnormally large leaf shows the same anatomical structure as does the

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1 Ueb. d. Beding. d. Konidienbildung bei Russtaupilzen. Flora, 1895, Bd. 81, p. 376.

2 Klebs, Beding. d. Fortpfl. bei einigen Algenpilzen. Jena 1896, p. 338. Congo red often exerts an arresting influence on the longitudinal growth of the membrane. Klebs therefore assumes that the cells treated with coloring matter only swell out like balls, but cannot be elongated, "the further result of this spherical form is, that, in the capacity for division, at first not arrested, new walls are laid on to the old cell wall, according to the principle of the least possible surface, and divide the content of the ball, independent of the longitudinal direction of the thread". For oblique division in Oedogonium compare the same author, loc. cit. p. 288.

3 Kny, Ueb. d. Einfl. v. Druck u. Zug auf d. Richtung der Scheidewand in sich teilenden Pflanzenzellen. Pringsheim's Jahrb. f. wiss. Bot., 1901, Bd. XXXVII, p. 55. Further literature references there.

4 Ueb. Wanderungen d. pflanzl. Zellkerns. Flora, 1901 Bd. LXXXVIII, p. 105.

small normal one. Homooplasia is opposed to the phenomena of the giant growth here described in so far that its products according to the definition always bear the character of abnormal tissue-formations. The latter will be the case, if the overproduction of the normal elements occurs only in narrowly limited places, or if only one of the tissue forms, or scattered forms, composing a leaf, a stalk, etc., are developed in abnormal abundance[1].

From the outset it must be noted that here, just as in the other groups which we have set up, no absolutely sharp demarcation can be drawn and that abnormal formations are not lacking, which furnish at the same time a transition from the phenomena of giant growth, the study of which is the task of morphologists, to homooplasias, which will be reported more closely in the following.

1. Localized tissue excrescences of an homooplasticcharacter, composed of the same histological elements as the original, are rare. A cross-section through a sugar beet (Beta vulgaris) is reproduced here, which continued its growth in thickness abnormally even in the second year, thereby developing several ridge-like tissue excrescences extending longitudinally. These extensive ridges are composed of normal layers of tissue. In figure 57, the concentric normal cambial rings are indicated in the center as well as those newly produced in
(140) the ridges. In a case closely investigated by de Vries[2] the formation of new cambial rings outside the latest ones of the first year, coincided with an arrestment of activity. The rings of the first year as well as the accessory ones of the second year were also only slightly lignified. The causes of the excrescences lie supposedly in an abnormally increased supplying of material.

Similarly the tissue excrescences, occurring on the leaves of Aristolochia Sipho and others, have been known for a long time. On the under side of the leaf blade, along the ribs, wing-like ridges, no thicker than the leaf, are produced, which like the normal leaf-blades are composed of epidermis and mesophyll and are traversed by vascular bundles. The question as

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[1] Virchow, (Cellularpathologie) uses the word hypermetry in a similar sense.

[2] Ueber abnormale Entstehung sekundärer Gewebe. Pringsheim's Jahrb. f. wiss. Bot., 1891, Bd. XXII, p. 45. There also statements on some of the tissue forms subsequently discussed by us and on the results of the "lengthened life-period". Further Rimpau, Das Aufschiessen der Runkelrüben. Landwirtsch. Jahrb., 1876, Bd. V, p. 43. Briem, Strohmer and Stift, Wurzelkropfbildung bei d. Zuckerrübe. Oest.-Ung. Ztschr. f. Zuckerindistrie etc., compare also Ztschr. f. Pfl.-Krankh., 1892, Bd., II, p. 239. Caspary observed on Brassica Napus (Eine Wrucke mit Laubsprossen aus knolligem Wurzelausschlag. Schriften Phys.-Oeken. Ges. Königsberg, 1873, p. 109), tuber-like swellings upon which were buds and which could develop bunched shoots with malformed leaves. The disease is hereditary as Caspary has shown. (Nypels described swellings on Beta of apparently varying structure. Notes pathologiques. C. R. Soc. Bot. Belgique, 1897, T. XXXVI, p. 183. Therein citations of literature regarding parasitic swellings of a similar kind.

to the conditions under which they are produced[1] has not been answered satisfactorily and would repay experimentation. Similar formations of ridges are already known in other plants; in the case of more vigorous development, they furnish a transition up to a duplication of the blade.

Hottas[2] produced experimentally on the roots of Vicia Faba, similar formations of lesser extent and simpler composition. If these roots were put in plaster casts, so that only little holes here and there above the tip made possible any further distension; these holes were filled by "correlative" growth in thickness of the roots. The form of the homooplastic excrescences corresponded to the form of the space at its disposal. It is possible in cases of this kind to speak of correlation-homooplasia, (see below).

Because of their external similarity to those above mentioned, the peculiar abnormal tissue excrescences may be mentioned here, which Nemec[3] observed on the roots of Cardamine amara. They are produced exogenously and are connected with the central bundle of the mother-organ by a procambial cord, without, according to Nemec, its leading in them to the formation of a true vascular bundle. Sometimes they bear root-hairs. Similar pathological structures occur also on the roots of Roripa. The conditions, with the fulfillment of which their formation is connected, are not yet known exactly.

II. The homöoplasias named in the following are characterized by the fact that only single tissue forms of an organ are super-abundantly developed and no production of local excrescen-
(141) ces, by which means the histology of the organ is altered. Indeed each tissue form can, under certain circumstances, undergo a homöoplastic formation.

1. A group well characterized physiologically is shown in those forms, in which the abnormally abundant formation of tissue is caused by some increased demand made upon it. Tissue formations of this kind which we will term work, or activity homöoplasias, (or hyperplasias), have long been known to physicians. Muscles of which more and more is required become enlarged, apparently by increase of their elements; as are also blood vessels upon which especially strong strain is put, after stoppage of other blood vessels, and the like.

We must make investigations to learn if plants are also capable of forming activity-homöoplasias.

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[1] Rudow (Einige Missbildungen as Pfl. herborgerufen durch Insekten, Ztschr. f. Pfl.-Krankh., 1891, Bd. 1, p. 332) thought mistakenly that he had recognized a mite gall in the Aristolochia ridges. Literature on these and similar structures is to be found cited in Sorauer, Handb. d. Pflanzenkrankh., 2. Aufl., Bd. 1, p. 239. Investigations made by Magnus (Sitzungsber. Prov. Brandenburg, 1877, Bd. XIX) show that with tissue excrescences may be united also phenomena of arrestment in the adjacent parts of leaves (Arrestment in the development in size of single mesophyll cells, scanty development of chlorophyll, and the like). In the cases which I investigated, the latter were always missing.

[2] Ueb. d. Einfl. v. Druckwirkungen auf d. Wurzel von Vicia Faba. Dissertation Bonn. 1901.

[3] Ueber schuppenförmige Bildungen an d. Wurseln v. Cardamine amara. Sitzungsber. Kgl. böhm, Ges. Wiss., 1901. N. VI.

In the first place, mechanical tissues as well as fibro-vascular ones deserve our attention, because they seem better fitted than other kinds of tissue for experimental action through increased demand upon them. Hegler was the first to attempt to cause the formation of mechanical tissue by increased mechanical demand[1]. The result of his investigations are the following: the working power of plant organs is favored by mechanical strain since the mechanical elements are then more abundantly formed than under normal conditions. Further, according to Hegler, the production of mechanical elements can be excited by mechanical strain even in those organs which normally develop none. I have mentioned already[2] that these statements of Hegler, at least on the plant organs which he investigated - petioles of Helleborus niger - are founded upon an error, since these even in normal individuals are not absolutely free from mechanical elements, as he thought them to be.

In order to be able to furnish a clear picture of the alteration and strengthening of the mechanical tissues, I have tried especially at different seasons of the year to influence tissue formation in Helianthus seedlings by constantly effective mechanical strain, - but unfortunately always in vain, so that I cannot report upon the amount of strengthening which the mechanical elements undergo according to Hegler. A thorough testing - the supplementing and correction - of his statements would be most desirable, and would undoubtedly lead to interesting conclusions. I wish, at this opportunity, to refer to the fact that increase in the trachae capacity of any plant part whatever can be produced in other ways than by increase of the mechanical elements alone or a better formation of the separate ones. As is well known, mechanical demand upon the strained plant body can change essentially the conditions of cohesion within it[3].
(142) It does not seem impossible, that mechanical demand can also modify the specific conditions of cohesion, in the cellulose wall, in the sense of an increase in mechanical effectiveness.

Wiedersheim[4] has recently investigated this thoroughly. He let a heavy weight (as much as 1.2kg.) act for months on branches of different species of weeping trees and compared the formation of the mechanical tissue in the strained and unstrained branches. In most of the objects - the weeping varieties of Fagus silvatica, Sorbus aucuparia and Fraxinus excelsior - no strengthening of the hard bast was demonstrable; only in Corylus avellana could an increase of the stereids be proved in the strained branches[5].

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[1] Pfeffer, Untersuch. R. Wegler's üb. d. Einfl. v. Zugkraften auf die Festigkeit und die Ausbildung mechan. Gew. in Pfl. Ber/ Sächs. Ges. Wiss,,1891, p. 638.

[2] Beitr. z. Anat. d. Gallen Flora, 1900, Bd.LXXXVII, p. 117.

[3] Compare for instance, Villari, Ueb. d. Elasticität d. Kautschuks. Poggendorf's Annalen d. Phys. u. Chemie, 1871,Bd.CXLIII.

[4] Ueb. d. Einfl. d. Belastung auf die Ausbildung v. Holz- und Bastkörper bei Trauerbäumen. Pringsheim's Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 41.

[5] The stone cells do not participate in the strengthening of the mechanical tissues. "We found stone cells formed in the same way in the laden as in unladen branches of Fraxinus, Fagus, Corylus (Widerscheim)". I cannot find in the negative results of the attempt to incite an increase of stone cells, any proof that, as Wiedersheim assumes, these cells possess no mechanical significance at least over against tensile strength.

Hanging gourd fruits, which develop more abundant mechanical tissue in their stalks than do the varieties which lie upon the ground, and the like have made it seem probable that an increase of mechanical tissue can be called forth by increased mechanical demand upon it. Wiedersheim's experiments have furnished exact proof of this. Future research will have to determine whether the tissues of different plant organs are equally suited for the formation of activity-hyperplasias, whether further only a few varieties are capable of it and whether finally by means of special conditions the organs, of which much is required, can possibly be made capable of an abundant development of their mechanical tissues.

A contribution on the last named case may be given here. Vöchting[1] reported recently on experiments with stalks of Brassica oleracea var. sabada (savoy) which were placed horizontally and strained at the tip by means of hanging weights. On the upperside of the branch, under the influence of the mechanical requirement, an activity-hyperplasia was produced by abnormally lively growth in thickness. In the present case only one side of the object under experimentation was taxed by the strain, - it would be conceivable that the very inequality of the conditions under which the different parts of an axis develop favors the production of an activity-hyperplasia.

Vöchting's researches have shown savoy to be a plant in which hyperplastic tissue changes occur on the side strained by bending. Future research will certainly make known other objects, in which the side taxed by the pressure reacts in the same way to the mechanical demand made upon it. In my opinion the formation of the red wood (bois rouge) of spruce and hemlock trunks favors this. This modification of the strengthening tissue, characterized by a red-brown coloration shows broader annual rings, richer in cells, than does the normal wood. It consists
(143) chiefly or exclusively of thick walled tracheids, which are somewhat shorter than the normal ones, often leaving perceptible intercellular spaces between them and conspicuous because of the spiral structure of their thickening layers. Hartig saw redwood regularly produced on the underside of horizontal branches and further in tree trunks on the side opposite the one exposed to the wind, when they were especially exposed to its action because of their position in the open, in short, in those places which were especially strongly taxed by mechanical pressure. In regions in which westerly winds prevail, the redwood side is always the one facing the East[2].

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[1] Zur experimentellen Anatomie. Nachr. K. Ges. Wiss., Göttingen, 1902, Heft 5.

[2] As the most important literature on redwood, compare Hartig, R., Das Rotholz der Fichte. Forstl.-Naturw. Zeitschr., 1896, Bd. V, p. 96; further Holzuntersuchungen, Altes und Neues, 1901. Compare also Mer, De la formation du bois rouge dans le sapin et l'Epicéa. C. R. Acad. Sc. Paris, 1887, T. CIV, p. 376. Cieslar, Das Rotholz der Fichte. Cbl. ges Forstwesen, 1896, p. 149. Anderson, Ueb. abnorme Bildung v. Harzbehältern und andere zugleich auftretende anat. Veränd. im Holz erkrankter Coniferen. Forstl.-Naturwiss. Zeitschr., 1896, Bd. V, p. 439. Observations on the influence of the wind on the unequal increase in thickness of trees extend back as far as Knight (1803), according to whose statements, the annual rings on the sides taxed mechanically (by bending) are broader than on the others. Compare further Büsgen: Bau u. Leben d. Waldbaume, Jena. 1897, p. 67, and the literature there cited.

The branches of conifers are known to be constructed hyponastically, i. e., excentrically, in such a way, that the horizontal underside of the branches is more strongly developed than is the upperside. I would like conjecturally to call attention to a connection between the excentric growth in thickness of normal parts of trees and the tendency toward (one-sided) activity-hyperplasia under abnormal conditions. If in conifers, the horizontal branches of which are developed more strongly on the underside,- the one taxed by pressure,- than on the upper side, it can be proved that the trunks also are developed hyperplastically on the side especially taxed by the pressure under abnormal conditions, then it may be conjectured that among plants provided with epinastic branches, whose branches therefore are more strongly developed on the side of the strain we may search for such as will, under experimental modification of the mechanical requirement, develop a reinforcement of the side strained. Trees with diplonastically constructed branches will possibly be able to react in the same way to the strain and pressure, due to a bending of their trunks, by reinforcing their tissues. It would be very desirable if, in connection with our knowledge concerning the formation of red wood, corresponding experiments could be made on deciduous trees and if some one would prove the influence upon growth in thickness caused by a bending continued over several years.

Besides mechanical tissues, vascular tissues also have an especial interest for us.

In order to increase the effectiveness of vascular bundles, which under normal conditions - to conclude from their extent, provide only for the transfer of moderate amounts, I cut through the mid ribs of young leaves of numerous dicotyledons which are pinnately ribbed (compare fig. 58) in the expec-
(144) tation that possibly the anastomoses well adapted for taking over the water connection between the upper and lower halves, (fig. 58a), would undergo a more vigorous formation than under normal conditions. The expected did not take place. In most cases the side ribs and their anastomoses are not capable of compensating for the intersected midribs nor of providing sufficiently for the upper half of the leaf. This either perishes entirely, or becomes discolored, or the leaf-development progresses abnormally, since leaves with disproportionately wide bases and stunted tips are formed (Populus pyramidalis). However, a more luxuriant development of the side ribs as activity-hyperplasia never took place in the plants which I investigated[1].

Further, I made girdling experiments with plants characterized by medullary phloem bundles (Eucalyptus, Nerium) but I could not prove that in girdled branches the latter had under-

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[1] In spite of the, at present, negative results, perhaps a continuation of similar experiments might not be undesirable.- At any rate, nature itself often makes experiments which, agreeing with what has just been described, prove that after removal of definite conducting paths, any provision on the part of the adjacent ribs and anastomoses does not take place. In leaves of the beech the helmet-like galls of Hormomyia fagi (compare fig. 58) which are produced on the side or midribs are often found very abundantly. The part of the blade provided for by the rib bearing the gall always bleaches very noticeably above the gall. If the gall is on a side rib, bleached stripes are produced; if on the main rib, a pale green, rhomboidal field is produced at the tip of the leaf,- a proof that the intact adjacent ribs and anastomoses are not in condition to provide sufficiently for the areas lying above the gall.

gone an especially strong development, or had become fitted to replace the lost peripheral phloem bundles[1].

The observations of deVries and Vöchting furnish valuable conclusions. DeVries (loc. cit.) describes a peculiarly abnormal potato tuber, from which three well-leaved sprouts were produced, which, however, lacked stolons. Two other eyes of the mother tuber, however, produced stolons without the requisite leaf-shoots. "The nutritive substances formed in the leaves did not find on the bark of the stalk the usual place of deposition, and were used successfully only in those tubers which bore sto-
(145) lons. Apparently for this purpose they had to transverse the old tuber". The vessels here made use of had undergone a strikingly vigorous development:- "but had not attained to the formation of a continuous woody-layer, although several bundles had united into groups. Each single bundle, however, had been developed to a degree not otherwise attained in potatoes.-- The wood consisted of wood-fibres and ducts arranged in rows, which usually showed a very distinct reticulated wall-formation. The phloem bundles showed a corresponding development, but did not noticeably differ in structure from the primary phloem". This description by deVries does not decide the question whether an activity-hyperplasia is actually present in the hyperplastic vascular bundles which he observed, or not; i. e., whether increased demand has caused the abnormal development of the vascular tissues, or whether probably some other reasons, unknown to us, have caused the abundant formation of their vascular bundles before the sprouting of the tubers. Occasionally even in ungerminated tubers one happens upon powerfully developed bundles or groups of bundles, which only with difficulty may be proved to be activity-hyperplasias.

Vöchting's[2] experiments furnish supplementary data, since they prove that by means of a definite kind of experimental interference, hyperplastically developed vascular bundles may actually be produced. He succeeded in interpolating the potato tuber as an element in the potato plants grown from it. The tubers were planted upright in the ground, to half their depth, and either developed leaved shoots above the ground and stolons with abundant roots below it, on which new tubers were formed, or the parts above ground were caused to form roots, by suitable expedients; the formation of stolons, however, was possible only on the parts under the ground. In the latter case the current of the assimilate flowed through the tuber to the newly formed stolons and daughter tubers; in the former the current of water flowing from the root-bearing stolons to the leaf-shoots traversed the old tuber the length of life of which was in both cases appreciably increased. The anatomical changes in the vascular bundles of the tubers correspond in all essentials to deVries' discoveries. Like the potato tubers those of *Oxalis crassicaulis* may be interpolated in the main stock of the newly produced plant.

Vöchting assumes that, in the abnormally constructed tubers which he investigated, the current of water and of nutritive substances caused the increase of the vascular elements, that further the increased mechanical demand also caused the increase

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[1] My experiments were interrupted after possibly a year. I consider it probable that positive results would have been attained in a longer experimental period.

[2] Ueber die Bildung der Knollen. Bibl. Bot., 1887, Heft 4, p. 11 ff. Zur Phys. der Knollengewächse. Pringsheim's Jahrb, f. wiss. Bot., 1900, Bd. XXXIV, p. 15 ff.

of the mechanical elements,- the tubers interpolated in the main stock of the plants had to carry the weight of the parts of the plant above ground. Accordingly, the tissue-formations here described would have to be added to the list of activity hyperplasias. This explanation is undoubtedly very interesting, yet, it seems to me that still other possible explanations should
(146) come under consideration here. The peculiar method of experimentation lengthened the life period of the potato tubar,-already emptied,- far beyond the normal one, so that a demand was made upon the different tissues of the tuber for a very much longer time than under normal conditions. Evidently continued demand does not of itself mean the same as increased demand. It might well be possible that even "continued" demand is enough under certain circumstances to incite the abnormal formation of secondary tissue, as observed by "Vöchting.

I would like here to call attention again to the experiments of Meer[1] who found leaves cut from Hedera helix forming roots and living for years. Secondary tissues were formed in the petioles by which the vascular bundles originally separated were united into a cord of tissue. It is absolutely not probable that the new formation of ducts etc. is here to be traced to an increase of the use of water, etc. To me the supposition seems better founded, that the continued demand made upon certain tissues, as a result of an abnormally long period of life, caused their hyperplastic formation. Yet do we not find that many perennial plants in the normal development of their parts under ground increase regularly, by cambial activity, their tracheal and mechanical tissues, corresponding to a "continued" demand made upon them, although the extent of the shoots developed yearly by them and the functional demand made upon them by these remain approximately equal[2].

In Vöchting's experiments, the conditions are in so far the same that tissues determined by them were kept alive longer than is usually the case under normal conditions. Here also a "continued demand" is made, with which there is also connected an "increased demans". The conditions are therefore extraordinarily complicated. It will not be easy to decide whether the reinforcement of tissues observed by Vöchting in Solanus tuberosum, etc. are to be put on an equal footing with those described by Mer or whether the "increased" demand was the determining factor of their production.

Conditions are much simpler when it is possible to bring about an abnormally abundant formation of vascular bundles in organs without lengthening the period of their life beyond the normal. Vöchting made experiments of this kind on dahlia tubers. These were planted in an upright position and, in spite of the unusual conditions, they rooted well, developing shoots in which a part of the stem was replaced to some extent by a piece of the root. Tubers, forced in this way to a greater mechanical work and through whose vascular bundles the whole amount of water

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[1] Bull. Soc. Bot. France, 1879, Bd. XXVI, p. 18.

[2] Increase of the tracheal and eventually also of the mechanical elements, as a result of continued (not increased) requirements, will occur probably also in those one-year old plants, whose shoots, used as stock, below the scion become two or several years old. (Compare Lindemuth, Das Verhalten durch Kopulation verbundener Pflanzenarten. Ber. d. D. Bot. Ges., 1901, Bd. XIX, p. 515). Unfortunately no suitable material has been accessible for me to test this question.

(147) necessary for the shoot was conveyed, contained abundant ducts and libriform fibres and thick-walled, pitted wood parenchyma cells. A comparison with equally old "normal" root tubers demonstrates that in this present case "continued" demand can not have incited the abnormal formation of tissue. In the abnormally developed dahlias which Vöchting described there clearly exists an effect of "increased" demand upon the tissues - an activity-hyperplasia.

Similar complications, making more difficult an understanding of the effective factors, may be found in many galls. If these are produced on petioles, the vascular tissue below them in the stem is often increased. In our native oaks various cynipides, most frequently Spathegaster baccarum, cause large, round galls on the staminate inflorescences. The axes bearing the galls not only live longer than normal ones, but are also distinguished by a secondary coalescence of their vascular tissue. The assumption that the increased mechanical demand and increased supply of materials and water have given rise to the described changes in tissue, is especially clear here; nevertheless, the possibility exists that the same secondary tissues would be found also if, in some other way and without a simultaneous increased functioning of the tissues concerned, it were possible to lengthen the life period of the inflorescence axes.

The histological structure of the abnormal tissues just described, reminds us that no sharp boundary may be drawn between homöoplasias and heteroplasias. Holding more strictly to the proposed principle of division we would have had to defer many a hyperplasia discussed in this section to the next one. As mentioned already the red wood, for example, does not consist of entirely normal elements since its cells are somewhat shorter than normal ones. In the vascular bundles developed in abnormal abundance, which Vöchting studied, tracheids of short cylindrical or barrel-like form occur, the libriform fibres are rather short etc. The abnormal coalescence of the tissues is therefore composed of elements which remain below the normal in their size development. They show the same variations from the normal cell structure that we shall find later coming into effect more strikingly in "kataplasmas".

On the other hand, Vöchting proved that in the abnormally developed vascular bundles of Oxalis crassicaulis, elements may be found in this tissue concrescence which are foreign to the normal tuber. Besides wood parenchyma cells, libriform fibres are also produced. In this case therefore the abnormal tissue displays a more abundant differentiation than does the corresponding normal one. We will find many differences of a similar kind in prosoplasmas.

If, in spite of the described structural differences, I have included all under homöoplasias, it was because the existing differences seemed too slight for me on their account to have wished to disorganize a group, well characterized physi-
(148) ologically. We find, however, often in a normal development of the vascular bundles, tracheal elements develop first of all, and then, by continued growth, wood fibres and wood parenchyma cells.

2. We speak of correlation-homöoplasias when, as a result of locally effective arrestment in growth, its localized furtherance takes place elsewhere, which leads to homooplastic changes

of tissue. Boirivant's[1] experiments on defoliated shoots are very instructive. The assimilatory tissues of the bark were increased "correlatively" in the shoots. Recently K. Braun[2] has made similar experiments and proved in Aconitum Stoerkianum, Syringa vulgaris, Corylus avellana var. atropurpurea, Rosa centifolia and others, an increase of assimilatory tissue, the number of layers of which at times was doubled. In Lamium orvala and others there was a striking increase of chlorophyll grains[3].

3. The abnormal tissues occurring on injured plant organs are usually of an heteroplastic character. I know of only one case of callus homooplasia. Schilberszy[4] succeeded in stimulating an increase of the vascular tissue in stalks of Phaseolus multiflorus through injury. This occurred because "the cell groups, lying close to the phloem bundles, therefore, those adjacent to the innermost layers of the parenchymatic primary bark, became adjusted for division, after some preceding injury, (by an interruption of the vascular bundle cylinders, closing upon one another like rings). Thus they took the form of secon-
(149) dary meristem." The newly produced meristematic zone acts like the cambial, producing xylem and phloem. Figure 59 shows part of a cross-section through a Phaseolus stalk. Outside the hard bast bundle are visible the newly produced xylem and phloem.

We arranged the material of our last three sections from an etiological point of view, but in them surely have not named all the factors, by which homöoplastic formations of tissue can be included in any one of the three previously named groups, the products of which, as I suppose, might have shown an homöoplastic character. In places on the laterally compressed internodes, the cells of the permanent tissue were incited by the force of compression to a growth perpendicular to the direction of the pressure and also to repeated cell division.

Kny observed similar abnormal division under similar conditions, in the pith of Bryophyllum calycinum and Begonia[5].

I know of no positive case where, by the action of foreign organisms, homöoplastic excrescences of tissue - "gall-homöoplasias" - would have been produced. In all galls produced by abnormal cell division, we are concerned with heteroplastic tissues, differing from the corresponding normal tissues in the nature of the differentiation and the volume of the separate elements,- when the fundamental tissues are simpler histologically, this may often be the only difference.

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[1] Boirivant, Rech. s. l. organes de remplacement chez l. pl. Ann. Sc. Nat. Bot., 1897, VIII. Sér., T. VI, p. 307.

[2] Ueber Veränd. im Gewebe entlaubter Stengl u. Zweige. Dissertation Erlangen, 1899.

[3] One may conclude upon a correlation-effect in the abundant formation of trichomes on the inflorescence stalks of Rhus Cotinus, whose bloom has not been fertilized. Indeed this formation of tissue should not be designated as "abnormal".

[4] Künstlich hervorgerufene Bildung sekundärer (extrafasciculärer) Gefässbündel bei Dikotyledonen. Ber. d. D. Bot. Ges. 1892, Bd. X, pc 424.

[5] Ueb. d. Einfl. v. Zug. u. Druck auf d. Richtung d. Scheidewände in sich teilenden Pflanzenzellen. Pringsheim's Jahrb. für wiss. Bot. 1901, Bd. XXXVII, p. 55.

We term heteroplasia each quantitative increase of an organ, in which, by abnormal cell division, tissues are produced, the single elements of which do not resemble normal ones. Thereby either whole organs, leaves, shoots, etc.- are transformed, or only parts of them, so that new tissue formations rest like an appendage upon the mother organ.

If the tissue of the heteroplastically changed organs and parts of organs be compared with corresponding normal tissues, differences will be found in more than one connection; the abnormal tissues vary from normal ones in regard to size of the single elements, as well as to the degree and kind of differentiation.

So far as the size of the single cell is concerned, it is easy to assume that abnormal increase of the cell numbers takes place at the expense of the cell size, in such a way that single elements of heteroplastic tissues do not attain their normal size. In fact relations of this kind seem to exist in many
(150) cases. Hartig[1] observed that broad, many-celled annual rings, consist of smaller (shorter) cells than do the inner ones with fewer cells. The callus, produced by abundant cell division after injury to living plant tissue, is composed at times of smaller cells than those of the ground tissue, etc. We shall not venture to attribute especial significance to this connection between cell number and cell size; in a very large number of cases the abnormal tissue is composed of larger cells, often indeed very much larger, than the normal tissue of the ground tissue.

Much more important are those differences, which make evident the differentiation of tissue in normal and in abnormal parts. As shown above, we shall be concerned with some tissues, which are more simply constructed than the corresponding normal tissues and with others in which we may recognize processes of differentiation in the formation of their single cells and the distribution of their different elements; which processes of differentiation, however, are not manifest in the development of the corresponding normal tissue. We will term heteroplastic tissues of the first kind kataplasmas, those of the second prosoplasmas.

Kataplasmas and prosoplasmas are not only distinguishable on the basis of an histological consideration, but are characterized also as independent groups by their external form. Kataplasmas show no constant proportion of size and form, the same abnormal tissues occur now as deformations of the whole organs, now as localized excrescences. In prosoplasmas, however, we find the "diseased appearance" always characterized by the definite size and form of the tissue excrescences; forms conspicuous because of a high, ever recurring organization, are not at all rare. The difference in form is connected most closely with the developmental period of the heteroplastic tissues. We find many kataplasmas of which the developmental period vacillates within very wide boundaries, in many cases we speak of it as (theoretically) unlimited. In prosoplasmas, however, the duration of the development of each single form may be most exactly determined as to weeks and months. The differences,named, for their part, may be explained, at least in a measure, by theetiology of the various abnormal tissues, which are partly caused by long persistent or permanent stimuli, partly by stimuli of a short duration constantly effective.

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[1] Holzuntersuchungen, Altes and Neues, 1901.

Besides histology, we will have to take etiology especially into consideration in the detailed description of the different heteroplastic tissues and in the subdivision of our material. In this we shall be able„repeatedly to make the same groups as in the treatment homöoplastic tissues.

Activity-heteroplasias of course will not be described. All hyperplasias have been disposed of above which are produced by a greater amount of action and indicate a relation to heteroplasias through their slight histological variation from normally constructed tissues.

Correlation-heteroplasias, produced after local arrestment of growth, will need at least a short chapter.

Callus-heteroplasias (in the widest sense of the word) i. e. all those heteroplastic tissues which are produced by wound
(151) stimuli,are,very diverse and demand thorough discussion. We will have to describe in order the undifferentiated, homogeneous wound tissue or the callus (s. str.), the wound tissue resembling wood, the wound-wood, and that resembling cork,- wound-cork.

A new group must be taken into consideration here, for which no analogy exists among homöoplasies, that is the gall-heteroplasias produced by foreign organisms, the multiplicity of which exceeds that of all other tissues disclosed by the study of pathological plant anatomy.

There are various other heteroplasias - and doubtless future investigation will disclose still further forms - which may not be included in any one of the above named groups, based upon etiological considerations. Since we have learned nothing as yet of the causes of their production, I have set aside no separate chapter for them, but have discussed them in connection with those of the above named tissues, with which they best correspond histologically.

If we now ask, which role the kataplastic and prosoplastic processes of differentiation play in the groups just distinguished, the following becomes evident. The correlation-heteroplasias so far as yet known have the histological character of kataplasmas. The same is true ofcallus, wound-wood and wound-cork. Among galls, we find kataplasmas and prosoplasmas which we shall have to discuss separately.

An equal consideration of the histology and etiology results in the following subdiwision of the material:

1. Correlation-heteroplasmas	)
2. Calluses	)
3. Wound-wood	) Kataplasmas
4. Wound-cork	)
5. Galls	(a. Kataplasmas
	(b. Prosoplasmas

1. Correlation-heteroplasmas

We speak of correlation-heteroplasmas if the normal growth of any plant is arrested at its vegetative points by any factors whatsiever, wherever under the influence of the unused nutritive materials, some part of the plant body is incited to abnormal growth,- to the production of abnormal tissue.

The simplest process by which we can arrest the normal growth in plants consists in destroying one or all parts of the vegetative tips of their shoots. If correlation-heteroplasmas are then produced, their formation results after the injury to be sure, but not because of it. No doubt exists that the same heteroplasmas are also produced when the normal vegetative points continue to live, if these are kept from further development, perhaps by being put into plaster casts. They may not be associated therefore with the callus formations named later.

(152) Vöchting has published valuable data on correlation-heteroplasmas[1].

If the inflorescences and all axillary buds were removed from vigorous kohl-rabi plants (Brassica oleracea f. gongylodes) the leaf cushions swelled gradually to extensive bodies, possibly to 2cm. wide, which "had been formed from the parenchyma of the bark of the cushion and from the vascular bundles running through it. These were formed in an unusual way and had developed partly to round, vigorous bodies covered all over with cambium. In the vascular parts, the tissue produced from the cambium consisted of thin walled elements, through which passed rows of small ducts. The abnormal tissue was distinguished from normal tissue by the absence of mechanical elements and the narrowness of the lumina of the ducts.

In cutback Helianthus plants analogous conditions may be found, "here too a significant development of the parenchyma and a retrogression of the mechanical elements is found in the stalk," especially in the upper part of the stem. In the lower part hollow cells are also produced after the operation but these are shorter than normal ones. On all sides a bending and twisting is frequently found. Vöchting found tuber-like swellings produced on the roots of decapitated Helianthus plants.

In the aerial runners of Oxalis crassicaulis, which are filled with reserve stuffs, are robbed of their apical cells and all axillary embryonic sprout cells, heteroplastic swellings are produced by the swelling of the leaves and internodes. According to Vöchting the cells of the fundamental tissue participate in the new formation chiefly by enlargement; the vascular bundles have fewer ducts than normal ones, but the sieve tubes are richly developed and at times extensive parenchyma outgrowths lie between xylem and phloem. Vöchting at times observed bi-collateral bundles in the abnormal tubers[2]. The development of collenchyma was absent in the stem, which had become inflated to a tuber, the mechanical elements usually accompanying vascular bundles were few or entirely lacking. I will return later to the noticeably large and irregularly formed starch grains, which fill the "leaf tubers" in especially striking forms. (Chapter VI, I).

It seems possible that cells of a permanent tissue may also be "correlatively" incited to growth and division.

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1 Zur Physiol. d. Knollengewächse. Jahrb. f. wiss. Bot. 1900, Bd. XXXIV, p. 1. - Zur experiemtellen Anatomie. Nachr. K. Ges. Wiss. Göttingen, 1902. Math.-naturw. Kl., Heft 5.

2 Abnormal vascular bundles of the same kind may be found in many galls (prosoplasmas), see below chapter V, B, 5.

From the statements of Vöchting here quoted, it is obvious that the tissue excrescences which he observed should be ascribed to kataplasmas.

Sachs[1] was the first to produce correlation-heteroplasmas experimentally. "If all vegetative sprout points be removed from vigorously growing pumpkin plants (Cucurbita mixima) a very remarkable phenomenon occurs which is as yet unexplained,
(153) the embryonic root cells, present in the tissue of the stem at the right and left of each petiole, grow out into short stalked tubers as large as hazel or walnuts, in which the root cap disappears and the vegetative point becomes irrecognizable, while the axillary fibro-vascular cord (the axillary cylinder of the root) is resolved into a circle of isolated vascular bundles, separated by ground tissue which contains chlorophyll." Sachs calls attention to the similarity between the normal structure of the axis and that of the abnormal Cucurbita tuber; I think that no special conclusion may be drawn from this as to the character of the new formation. That roots may become green is a wide-spread phenomenon, already described above (p. 56). The other histological characteristics, distinguishing the tubers from normal roots, seem to me connected with the overproduction of undifferentiated parenchyma, recurring in so many heteroplasmas.

Further investigations will show whether all plants can at will be brought to the formation of correlation-heteroplasmas or whether those plants tend especially to this kind of excrescence which form parenchymatic, little differentiated tissue-masses ("tubers") even in a normal course of development. That the ability to develop correlation-heteroplasmas is not restricted to tuberous plants is shown by the cases just discussed.

C. Kraus[2] using Helianthus, attempted to influence the processes of growth by removing the apices of the plants under experimentation. According to him, wart-like petiole excrescences are formed on the stalks which have no inflorescences. C. Kraus also makes some statements concerning the anatomical structure of the plants operated upon. In similar experiments Wollny[3] found that the axillary buds were transformed into tuber-like rolls.

It must be left undecided whether the "gnarled tubers", occurring on various Eucalyptus species, are to be reckoned among correlation-heteroplasmas. Some notes concerning these may be found in section 3, which treats of wound-wood.

2. Callus

Leaving out of the question the products of the processes of restitution, we have termed all cell and tissue forms, produced after and as a result of injury, callus formations in the widest sense of the word and have spoken of them repeatedly. In many plants and plant organs only a metaplastic change

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[1] Gesamm. Abhandl., Bd. II, p. 1172.

[2] Künstl. Beeinfl. des specifischen Bildungsganges von Helianthus annuus durch Entblätterung u. s. w. Forsch. Geb. d. Agrikultur Physik, Bd. IV.

[3] Einfl. d. Entgipfelns der Pfl. auf deren Entwickelung und Produktionsvermögen. Ibid., 1885, Bd. VIII, p. 107.

of the existing cells was incited by the injury (callus-metaplasia); in others the cells laid bare showed an abnormal growth and were changed into voluminous vesicles and sacs (callus-hypertrophy). In the preceding section A, it was shown that even an increase of the normal tissue can result from wound stimuli (callus-homöoplasia). Those cells are most
(154) abundant in which after injury a heteroplastic tissue is produced by cell division (callus-heteroplasia).

In the majority of cases of callus hypertrophy (see above p. 92) it was proved that the resulting large cells remained below the normal cells of corresponding tissues in internal formation; the chlorophyll content being usually lost in hypertrophy. In rare cases the occurrence of new characters was associated with the abnormal growth (p. 95).

Similar conditions exist in heteroplasias incited by injury. Excrescences arise, which are composed of cells of the simplest form, very little differentiated, and are distinguished by this means from the ground tissue. They are all characterized therefore as kataplasmas.

Kataplasmas, produced after injury, differ very greatly among themselves. Either tissues resembling cork are produced, termed wound-cork, or those similar to wood, called wound-wood, or nearly homogeneous parenchyma masses which are composed mostly of very thin walled, undifferentiated cells, often absolutely irregularly connected. We term tissue of the last kind simply <u>callus</u>. Also all plants and organs are not capable of producing all three tissue forms after injury.

We will begin our description with the homogeneous, parenchymatic "callus".

We find representatives of very different plant groups capable of forming callus tissue; algae and fungi often form it, the vascular cryptogams less often. The callus tissue of the phanerogams is of great significance; gymnosperms, monocotyledons and dicotyledons, herbaceous and woody plants may form it after injury. We shall have to study especially thoroughly the callus tissues of higher plants.

First of all some examples may be given, from the list of <u>cryptogams</u>.

<u>Algae</u>, at least the larger tissue-forming marine species, form tissue excrescences of simple histology, besides the well-known adventitious shoots. The tubercle-like callus in these consists mostly of cells of one kind or of cambium and bark layers with little evident difference. The cells are often arranged in radial lines; at times they are somewhat larger than the cells of the mother-foundation. Tubercles of this kind occur in Fucus, Polyides, Dellesseria, etc.[1] I found swellings in Laminaria which grew out to the size of peas, possibly attributable to injury. I consider it very possible that the tubercles, described by Schmitz[2], which he traced to bacterial infection, have been produced by injury and cicatrization and that

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[1] Küster, Ueb. Vernarbungs -u. Prolifikationserscheinungen bei Meeresalgen. Flora, 1899, Bd. LXXXVI, p. 143.

[2] Ueb. knöllchenartige Auswüchse an d. Sprossen einiger Floriden. Bot. Ztg., 1892, Bd. L, p. 624.

(155) the bacteria wandered subsequently into the porous callus tissue[1]. The cells of the algae tissues when wounded are very frequently stimulated to cell division without the formation of extensive swellings. The cicatrization tissue formed on the "leaves" of Sargassum shows some correspondence with the callus of higher plants.

Fungi also form galluses, but, as it seems, less easily than algae. Hennings[2] observed in xylaria a ball-like callus-swelling on the stroma.

Among vascular cryptogams, various species of Selaginella may easily be brought to the formation of callus. The cells of the parenchyma, filling the passage surrounding the vascular sheath, are incited to abundant division by wound stimuli[3].

Woody plants, especially among phanerogams, have been studied often and thoroughly as to their formation of callus. If cuttings of rose, poplar or willow branches of any length whatever are made and left undisturbed in moist air and under sufficiently high temperature, after a few days a ring-like tissue excrescence is formed on the cambium on the cut surface. This enlarges rapidly, spreads out like a roll on the cut surface and unites eventually with the same kind of new formation, which grows out from the pith and bark. These rools of tissue have been known as callus for a long time. This is true also of their tissue construction as stated above. Sooner or later the callus discontinues its growth and in many species produces new vegetative points, - favorable outward conditions being taken for granted. Thorough anatomic studies were made especially by Treoul Cruger and Stoll[4].

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[1] Also in the swellings observed by Barton (On certain galls in Furcellaria and Chondrus, J. of Bot., 1901, Vol. XXXIX, p. 49) a callus tissue maybe involved, which was produced through the grazing of animals and is inhabited by them. (N. B. Barton's statement that Florideae starch, occurring in the "galls" of Furcellaria, is lacking in the normal tissues of the alga, is based upon an error).

[2] Ueber Pilzabnormitäten. Hedwigia, 1901, Bd. XL, p. 136.

[3] Molisch Zur Kenntn. d. Thyllen nebst Beob. üb. Wundheilung in d. Pfl. Sitzungsber. Akad. Wiss. Wien, 1888, Bd. XCVII, Abt. 1, p. 264.

[4] Trécul, Reproduction du bois et de l'écorce. Ann. Sc. Nat. Bot., Serie III, 1853, T. XIX, p. 157. - Crüger, Einiges über die Gewebeveränderungen bei der Fortpflanzung durch Stecklinge. Bot. Ztg., 1860, Bd. XVIII, p. 369. - Stoll, Ueb. die Bildung des Callus bei Stecklingen. Bot. Ztg., 1874, Bd. XXXII, p. 737. - Rechingar, Unters üb. d. Grenzen d. Teilbarkeit im Pflanzenreich. Zool. - Bot. Ges. Wien, 1893, Bd. XLIII, p. 310. Compare further the summarizing reports by Sorauer (Handb. d. Pflanzenkrankh., 2. Aufl. Bd. I, p. 561, 658) and Frank (Krankh. d. Pfl. 2. Auf. 1, Bd. 1, p. 63) as also the authors named in later notes. The new work by Löckell (Die ersten Folgen d. Verwunduhg d. Stengels dikotyler Holzgew. u. s. f. Jahresber. 10. Realschule Berlin, Ostern 1901) may boast of but little clearness.

The prominent activity of the cambium in callus formation, determines the fact that the callus, at least in its first stages, usually appears in the form of a ring on the cross section of the shoot. In cuttings of many plants, the production of callus is relatively scanty, so that in them it
(156) never passes beyond the stage of a flat, ring-like roll. In others, as Populus, Rosa, Catalpa and many others, the callus continues to grow for a longer time, especially if the cuttings are kept in moist air. The fact that callus tissue never has a specific form is also important. The luxuriant new formations, produced, for example, on cuttings of Populus pyramidalis (compare fig. 60) assume very different forms, even when allowed to develop freely, and are covered with large and small protuberences, irregularly distributed. Besides this, from the very beginning, the production of callus in many cases does not take place equally strongly on all parts of the cut surface,- often indeed it may be entirely lacking in places. The space conditions of the callus often determine its form; the callus masses fill out all splits in the wood of the cutting, etc. Figure 60B shows a callus which was developed under a glass plate. Since development in a longitudinal direction was thus prevented, it spread out sidewise without being distinguishable in any way from callus tissue which develops undisturbed. The same is true of the callus tissues of herbaceous plants. Figure 61 shows the callus from a stalk of Lamium orvala, the plant which among herbaceous plants produces the largest callus-rolls of which I know. The irregular, wax-yellow callus masses, as large as one centemeter which are produced on cuttings of Catalpa syringaefolia are very striking and resemble coralloid branches cones.

In rare cases the callus appears in the form of algae-like threads, as Stoll for example has observed in Tradescantia. At this point, I would like to mention the hair-like structures found by Sorauer in the core of "woolly streaked" apples, (loc. cit. p. 296), which might possibly be attributed to injury. (Compare fig. 68). Massart also (loc. cit. p. 56) observed the same structures. I will return later to these.

The period of development of the callus varies with the controlling external conditions and the nutritive condition of the object under investigation.

Origin of the callus

Callus tissue can be produced on all organs, on roots, axes, and leaves. Yet all parts of all plants are not capable of forming it.

Further, all living elements of exposed tissue can be incited to growth and division through injury so far as their membranes have not become lignified, and therefore incapable of surface-growth. An exception to this is made by wood parenchyma cells which, as seen above, are incited only to growth by wound stimuli, overlooking some very rare division. Usually in wounded organs and isolated pieces of organs of any definite plant species, only single tissue forms are caused to form callus.

The productive power of different kinds of tissue varies greatly. In those rare cases in which the epidermis acts at all it produces only very small amounts of tissue. The chief amount of callus is produced by the cambium on pieces of stem or stalk[1]. In many cases indeed this is the only tissue which is able to produce it. Next to the cambium, the primary and secondary bark tissues, as well as the pith, come under consideration, which can also furnish considerable amounts of tissue - often the activity of the bark is scarcely less than that of the cambium.

The formation of callus therefore furnishes proof that through injury, not only meristematic tissues, such as the cambium, can be brought to an increased and abnormal activity, but the cells of the permanent tissue as well, such as bark and pith, can be incited to extensive growth and abundant division.

Life history of the callus

The life history of the callus will have to be studied separately in the various tissues producing calluses. As a basis of our description, we will take first of all the phenomena observed on cuttings of woody plants.

The important part played by the cambium in the callus formation which has just been mentioned, has been thoroughly
(158) investigated by Stoll (loc. cit.) with cuttings of Passiflora quadrangularis. "After the lapse of 24 hours the cross walls of the cambial cells, bordering the cut surface and previously flat, had become curved outward,- when not cut to pieces. A stretching parallel to the long axis took place simultaneously with this outward curving, and after 24 hours more, a division over the cut surface by means of two or three cross walls". Further, "in the cambium a region of cells, capable of continually forming others by tangential and cross-division, had been differentiated over the cut surface, which formed the point of departure for all further growth from the cambium. The cells lying below this point undertook no new division, and were pushed away little by little toward the outside".

The investigations of Stoll (loc. cit.), R. Hoffman[2] and others, as well as my own, show that the cambial cells when dividing after injury, are not restricted to the mode of normal division but are capable of growth and division in every direction. It is certain therefore that the changed pressure conditions are of great significance. On the other hand it is scarcely possible to explain by these alone the phenomena of growth which follow injury[3]. The cell divisions leading to the formation of callus are very regular in those woody plants which form it quickly and abundantly. Therefore the processes are in detail as follows.

If cuttings of Populus pyramidalis and others are placed in water and covered with a bell glass, so that the upper end

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[1] Knowing the significance of the callus for the union of scion and stock, it is thus comprehensible, that plants with a cambial ring unite more easily when brought together, than plants without one (monocotyledons).

[2] Hoffman, Rob. Unters. üb. d. Wirkung mechanisch. Kräfte auf d. Teilung, Anordnung und Ausbildung d. Zellen u.s.w. Dissertation Berlin, 1885. - Schumann. Dickenwachstum u. Cambium Dissertation Breslau, 1873.

[3] Compare R. Hoffman, loc. cit.

extends above the water into the moist air, division takes place very soon in the cambial cells near the upper wounded surface[1]. They are divided by walls perpendicular to their long axis, producing thereby short prismatic elements. These, for their part, divide in an extraordinarily lively manner by forming tangential walls, causing an abnormally intensive growth in thickness of the cutting near the injury, although the bark pressure remains unchanged even in these places, or may actually increase as a result of the growth in thickness.

Figure 62 shows a longitudinal section through the upper end of a cutting made slantingly. A powerful callus ring has been developed on its cut surface. The cambium has been incited by the injury to extraordinarily abundant cell division. Not only directly on the cut surface, but even at a considerable distance below it, an abnormally lively gorwth in thickness has taken place, which acts most strongly at the cut surface, gradually decreasing toward the lower part, so that the cutting seems forced out to a club-like form at its upper end. With Th. Hartig, we can term the wedge thus formed between xylem and phloem the "Lohden Wedge"[2]. Above, on the cut surface, the newly produced tissue (C) is forced out in a ring-like roll.

(159) Anatomical investigation shows that, in the production of the new structure, the cambial cells have divided just as under normal conditions. The Lohden wedge consists of radial rows of cells the developmental homogeneity of which may be seen everywhere except in the upper cell layers and the convex ring-like roll. In this cell divisions may usually be seen in every possible direction but no longer with any regular arrangement in rows. Sections through very young callus tissue show, however, that no deviation from the normal is present, so far as the direction of the first divisions is concerned. The segmented cambial cells divide in a tangential direction parallel to their long axis. Cross walls arise later in the products of their division and are variously oriented. Figure 63 illustrates what has been said. The cambial cells directly at the cut surface (B) have perished, those following next have produced some few cells- by tangential division-, the next have divided very abundantly. The arrangement of the products of division makes it still possible to follow the life history. The outer parts
(160) of these complexes which are formed in rows, - in which cross division takes place in very different directions - help to make the outer visible callus roll; their inner parts, adjacent to the xylem, show regular rows with only parallel walls. Of the succeeding cell complexes - at the left in the figure - only the inner, regular sections are shown in the drawing. The illustration shows at the same time that the cells of the meristem of the medullary rays can participate in the formation of the callus, in the same way as do the adjacent segmented cambial cells.

The next illustration shows in longitudinal section the luxuriantly developed "Lohden wedge" (C) of an elm. The cells, so far as arranged in clearly recognizable rows, are indicated in the figure as curves in the "Lohden wedge". The lowest (innermost) of these curves are bent only slightly, if at all, the upper ones (outermost) on the contrary, are bent very strongly. Since the cells of the "Lohden wedge" not only grow in a radial

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[1] The investigations of the cambial products is made easier, if cross-sections are also made on <u>obliquely cut</u> cuttings (Compare fig. 62 and 63).

[2] Lehrb. f. Förster, 9 Aufl., Bd. I, p. 227.

direction but also in the direction of the long axis, it is evident that the radial cell rows curve out toward the cut surface, until they finally tear apart, as at z in the figure. Beyond this point of tearing, the cell divisions are very irregular[1]. In the callus of the elm here shown, however, the cell rows may be clearly recognized although they are turned toward the outside.

The further increase of the callus tissue is often brought about by the appearance of a new meristematic zone, the position of which may vary. In figure 64, at a-a, such an one is indicated.

In addition it should be emphasized that the youngest <u>bark</u> layers act just as do the cambial cells, - from which they may not always be sharply distinguished,- furnishing the same short-celled parenchyma as do the cambial elements. The conifers, so far as investigated, assume an unique position, in that the latest, unlignified elements of the <u>wood-body</u> are also incited to an analogous change by wound-stimuli. They divide and furnish parenchyma cells[2].

Figure 65, a tangential section, made above a girdling wound in <u>Abies cephalonica</u>, shows in its upper part normal trach
(161) eids with bordered pits, in its lower, parenchymatic cells, produced by segmentation of the young woody elements which have unbordered pits. The transition between the two zones furnishes some cells which show the character of tracheids in their upper parts, but in their lower ones, the pitting of parenchyma cells.

Not only the youngest elements of the <u>secondary bark</u>, of which we have just spoken, participate in the formation of callus, but at times all of its layers or at least the growths of the last few years. Of all the cuttings which I have investigated, those of Populus form the most abundant bark callus. Here, as from the cambium, regularly radial rows are also produced by tangential cell division, which curve out on the cut surface like rolls, as was stated above for cambial callus. (Compare fig. 66). The bark callus usually merges with the adjacent cambial callus into an homogeneous tissue roll, so that
(162) it is possible to determine only by microscopic investigation which part of a callus pertains to the bark or to the cambium and whether the former was at all active[3].

In plants with fixed medullary phloem, its cells may be incited by injury to division and the formation of callus. (Observations on Eucalyptus).

The <u>primary bark</u>, especially in Salix, passes over easily to the formation of callus. Only a few days after the injury,

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[1] The changed tensile and pressure conditions might not be without influence on the direction of the cell division.

[2] Mäule, Der Faserverlauf im Wundholz. Bibl. Botan,, 1895, Heft. XXXIII.

[3] Also in Populus, the participation of the bark in the formation of callus varies greatly in different examples; often it is entirely lacking. In one case, I saw the cambial callus only weakly developed, and the bark callus therefore excessively richly increased.

if kept in moist air, a glittering crystalline covering is formed from the callus tissue, which, in comparison with the new formations already described, does not exceed a relatively moderate amount. The cells, lying under the cut surface, are stretched perpendicular to the surface of the wound and divide repeatedly with irregularly oriented walls. Rows of cells belonging together developmentally generally are not formed here. I observed at times a predominant tangential division in the bark of young Sambucus sprouts.

To be sure the pith often increases but only rarely furnishes rolls of tissue as large as those on cuttings of Populus. In these from 10 to 12 days after the injury, a sheath-like knobbed callus mass, usually star-shaped, becomes visible, above the pith and is often greatly increased; the wounded surface of the xylem grows out toward the cambium like a wall and is united to it. It is clear from longitudinal sections that the uppermost cell-layers of the pith died after the injury and that those immediately underneath have been elongated perpendicularly to the wounded surface and have divided repeatedly. From the very beginning any definite direction of division is also absent here;- generally well arranged cell rows do not exist.

The epidermis becomes active only in rare cases. Stoll thinks it doubtful if it can ever participate in the formation of callus. Hansen observed divisions in the epidermis, however, which led to callus formation (Begonia). Further observations are reported by Massart, who proved a division of the epidermal cells in the stalks of Ricinus and Tinanthia (loc. cit.)[1]

Any ability to form callus may scarcely be spokem of in connection with the cells of the wood-parenchyma. As was thoroughly discussed above, the wood parenchyma cells, incited to growth through injury, almost always remain undivided. According to Molisch, division is known only in the tyloses of
(163) Cuspidaria pterocarpa and Robinia (compare above p. 102). This does not exclude the fact that tyloses occasionally become enlarged and, like the products of the cambium, the bark, etc. can curve out over the cut surface. In the cuttings of Platanus the cells grow out from the cut ducts in the form of gigantic pouches. The statements of Stoll that in Passiflora quadrangularis the tyloses grow out only from the ducts, and divide repeatedly outside these, producing a many celled callus, which unites with the callus of the cambium and of the pith, are based indeed upon an error and need testing. Tompa's[2] study throws light on the participation of the wood parenchyma

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[1] Hansen, Vgl. Unters. üb. Adventivbildung bei d. Pfl. Abhandl. Senchenberg Naturforsch. Ges. 1881, Bd. XII.- Massart, Cicatrisation chez l. végétaux. Mém. cour. etc. Acad. Belgique, 1898, T. LVII. - I must here leave open the question as to whether in the cases given by Massart, callus tissue or wound-cork is really concerned, we will discuss these again later. In the case investigated by Bretfeld (Ueb. Vernarbung und Blattfall, Pringsheim's Jahrb. f. wiss. Bot. 1880, Bd.XII, p. 133), in which theepidermal cells of the Clivia leaf divided, a formation of cork exists as the author emphasizes; perhaps similarly also in the cell division observed by Massart on the leaf of Banisteria argentea (loc. cit., p. 49).

[2] Soudoure de la greffe herbacee de la vigne. Ann. Inst. Ampélol. Budapest 1900, T. 1, No. 1.

of Vitis in the formation of callus. Also in roots rich in parenchyma, cases are not lacking in which the wood parenchyma after injury takes part in this formation. I have never as yet been able to observe division in the wood parenchyma of roots of Taraxacum.

If we again look over what has been said, we can make certain that, after injury, the cambium and secondary bark, corresponding to the normal dividing activity of the cambial cells, strive to form a tissue radially arranged. In the pith and primary bark of the objects investigated such a tendency was not found.

Petioles and leaves also often form abundant callus from their bark tissue and especially from their mesophyll. To me the callus excrescences formed on the petioles of Populus seemed especially striking because so abundant. The colorless tissue formed on the edges of wounds of leaf blades (Acer, Syringa, etc.) bears but slight resemblance to the normal epidermis with which it has been compared at times by various authors. The life history of the callus on leaves discloses nothing new. The extensive callus rolls deserve especial mention, however, which are produced in the leguminaceous cotyledons, rich in starch, after their removal from the axis. I found them becoming highly multicellular in Vicia[1]. Here the cells below the cut surface are also elongated perpendicularly to it and divide repeatedly without noticeable regularity[2].

In fleshy leaves, the burrows eaten into the mesophyll by insect larvae are not infrequently filled by a multicellular callus, containing chlorophyll, which distends the epidermis. Thus, in later stages, instead of the burrows, we find ridges on the leaf which are filled with callus. (For example, in Sedum spectabile, Brassica, etc).

(164) A thorough investigation of the changes to be found in leaves injured by mining insects might well be worth while. The conditions acting here on the injured tissue differ essentially, however, from those which come into effect after somewhat coarse interference on the part of the experimenter. Perhaps the reaction of the plant tissues is also correspondingly different.

The filling of the burrows with callus tissue is shown also by the tender masses in the wood of different trees, long known as "moon-rings". According to deBary's[3] description, they are composed of irregularly polyhedric parenchyma cells with thick pitted walls arranged irregularly. On account of their similarity to medullary-tissue, Nordlinger called them "medullary spots". Their histology, the irregular arrangement of their elements, and

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1 Since Van Tiegham (Rech. s. l. germination, Ann. Sc. Nat. Bot., 5me sér., 1873, T. XVII, p. 208) whose statements should be compared here, the fate of the isolated cotyledons has been especially investigated.

2 Further statements on callus in leaves also in Massart loc. cit., Blackman and Matthaei:- On the reaction of leaves to traumatic stipulation. Ann. of Bot., 1901, Vol. XV, p. 553. Aderhold, Ueb. d. Sprueh -u. Duerrfleckenkrankh. d. Steinobstes. Landw. Jahrb., 1901, Bd. XXX, p. 771 and many others.

3 Vergl. Anat. d. Veget. - Org., p. 507.

their passage-like course favors the explanation of M. Kienitz[1], who recognized in them, at least for Salix, Sarbus and Betula, callus filled passages of the larvae of some Diptera. Of course, even after other kinds of injury, the cavities[2] produced in the cambium can be filled with similar tissue.

Histology of the callus

As has been already emphasized, callus tissues are characterized histologically by the slight differentiation of their cells. In many kinds of cuttings the callus rolls consist throughout of the same kind of cells; they are constructed perfectly homogeneously. The separaate cells are always thin-walled, filled with a clear cytoplasm and an almost always colorless cell sap. In slow growing callus excrescences the tissue is usually small-celled and close, larger interstices are visible only in the outer cell layers. In those growing rapidly, the cells are usually large, loosely layered, separated especially in the outer layers by large intercellular spaces. In the callus of Cydonia japonica and others, I found that the tissue connection often became so broken, that the cells were almost completely loosened from one another. If callus tissues are left in the light, they become green; their chloroplasts, however, are always few in number, small and poor in pigment, on account of which the callus rolls are always a pale green, at times even more yellow than green, as in Catalpa.

No definite laws determining the proportionate sizes between callus cells and those of its mother tissue may be recognized. In Populus, for example, the cambial callus consists of cells, which are appreciably larger than those of its mother tissue, while the products of the pith are smaller than those of normal medullary cells.

A difference between the single cells is caused very often by the fact that some of them, - especially in the inner layer of the callus,- are changed to tracheids by reticulated thickening and lignification of their walls. Their formation may be traced especially clearly in the callus of poplar cuttings. Figure 67 shows part of a callus of Populus: - the delicate walled, irregularly arranged parenchyma cells with wide lumina enclose a tracheid with reticulated walls. Although in the
(165) "Lohden wedge", especially in its lowermost part, very many cells assume a tracheal character, tracheids are relatively rare in the upper callus roll. They are irregularly distributed in the undifferentiated tissue. Moreover, the under layers near the place of origin of the roll are usually more abundantly furnished with tracheids than the outermost ones. By the union of many tracheids, primitive vascular bundles and a wood-like tissue are produced, which will be spoken of later as wound-wood. The cells of the superficial layer of the callus never become tracheids.

It is now worth noticing, that not onlyd derivatives of the cambium may become tracheids, but that callus from the

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[1] Entsteh. d. Markflecke, Botan. Cbl., 1883, Bd. XIV, p. 21; there and in DeBary reference to older authors. (Th. Hartig, Kraus, etc.).

[2] Compare also Sorauer, Handbuch der Pflanzenkrankh., 2 aufl., Bd. 1, p. 382.

secondary bark and from pith also produces elements of the same kind. The same differentiation is undergone by the callus of injured cotyledons (Vicia, etc.), of petioles (investigations on Salix and Populus) and of roots (Taraxacum).

Next to the formation of tracheids, the development of an <u>epidermal tissue</u> is the most striking process of differentiation in the callus. This too may be studied in the callus tissue of poplar cuttings. Its outermost layers differ from the inner ones first of all by the greater volume of the single cells. These are forced out into the form of pouches or long sacs. Their walls, so far as they come in contact with the air, give the reaction of membrane-coverings which have become cork, since they take up Sudan III[1] abundantly and at the same time are colored with phloroglucin and hydrochloric acid, like lignified membranes. I do not doubt that the same substance (or a similar one) is the cause of these reactions, just as occurs
(166) in the "wound-gum" of very different plants[2]. On closer observation, delicate, pouch-like or semi-spherican, convex prominences become noticeable on the outer walls of the cells, which may consist entirely of a gum-like mass, the reaction of which we have just mentioned. Mellinck has also observed these in callus formations on the petioles of Nymphaea[3]. An especially good object for this investigation might be furnished by the "woolly stripes" of apples, which Sorauer[4] has described. The woolly stripes are produced on the innerside of the core; definite cell groups grow into thick little bunches of cell rows lengthened to look like threads, (compare fig. 68), "which differ from those surrounding them in their thinner wall-formation and pass over very gradually into the tissue of the fruit's flesh". On these cells, wart-like or knob-like "thickenings" of the cell wall appear, as is shown greatly enlarged at the left in figure 68[5]. The tissue described by Sorauer of which

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1 In using Sudan III, I generally proceed thus;- after leaving the sections some minutes in a dilute solution of the coloring matter, I then boil them in glycerine on the slide.- During the boiling, the membranes which have become cork are colored a strong red.

2 Compare especially Prillieux, Et. s. l. formation de la gomme d. l. arbres fruitiers. Ann. Sc. Nat. Bot. 1875, 6me ser., T.1, p. 176. Frank, Ueb. die Gummibildung im Holze u. deren physiol. Bedeut. Ber. d. D. Bot. Ges. 1884, Bd. II, p.321. Tamma, Ueb. Schutz-u.Kernholz, seine Bildung u.s.physiol.Bedeutung. Land u.Kernholz d. laubbäume. Pringsheim's Jahrb. f. wiss. Bot. 1888, Bd. XIX, p. 52. Molisch, Z. Kenntn. d. Thyllen etc. Sitzungsber. Akad. Wiss. Wien, 1888, Bd. XCVII, Abt. 1, p. 264. Lopriore. Ueber die Regeneration gespaltener Wurzeln. Nova Acta Leop.Carol. Acad. 1896, Bd. LXVI. Kieler, Die gummösen Verstopfungen des Zuckerrohrs. Beitr.wiss.Bot.1898, Bd. II, p.29 and many others.

3 Zur Thyllenfrage. Bot. Ztg., 1886, Bd. XLIV, p. 745. I think it more correct to place the often multicellular forms observed by Mellinck, in wounded leaf stalks of Nymphaea among callus forms, rather than among tyloses.

4 Handb. d. Pflanzenkrankh., 1886,2 Aufl., Bd. 1, p. 296.

5 Apparently the same forms can occur also in normal tissue. Jost found them in the aerial roots of <u>Phoenix spinosa</u>, (Beitr. z. Kenntn. d. Atmungsorgane d. Pfl. Bot. Ztg., 1887, Bd. XLV, p. 601), Noack in the intercellular spaces in the roots of various orchids (Ueb. Schleimranken in d. Wurzelintercell. einiger Orchideen. Ber. d. D. Bot. Ges., 1892, Bd. X, p. 645).

(167) the original causes of production are not yet known, resembles many callus tissues[1] (see above). On this account I ventured to mention it at this point.

In the outer cell layers of most callus formations a cork meristem is produced sooner or later, the products of which will be termed wound-cork. We will return to this later.

Crystals - - isolated crystals like glands,- may often be met with in callus (for example, in Populus, Fagus, Corylus, and many others); usually, however, in lesser quantity than in normal tissues. Raphides may be found (according to Sorauer) in the callus of Fuchsia. According to Stoll (loc. cit.) stone-cells are formed in the callus of Camellia japonica, "gum passages" in Hibiscus reginae. I observed the formation of anthocyania, for example, in the callus of Populus. According to Rechinger[2] the callus of the roots of Armoracia rusticana is rich in starch. Vacuoles of tanic substances are very noticeable in the callus of many foliage trees. I found latex tubes in the callus of Taraxacum roots. Differentiations may, therefore, be found in callus similar to those which we are accustomed to find in the normal tissue of the plants concerned, only very much more weakly developed - - corresponding to the character of all kataplastic tissue.

Massart (loc. cit.) was the first to treat the question of nuclear division in callus tissue, which, in the cases investigated, only exceptionally contained more than one nucleus in each cell. In Ricinus, Cucurbita and Tradescantia he found that, in the majority of cases, direct nuclear division took place after injury. His supposition that the nuclei in all wound-tissues divide amitotically has been disproved by Nathansohn[3]. Nathansohn found that only mitosis occurs in the callus of halved roots of Vicia Faba, but mitosis as well as amitosis in that of poplar cuttings.

Conditions of callus formation

It seems a matter of course that different plants should behave very differently in regard to the production of callus. The time which the injured plants need to develop it, as well as the amount formed in different plants fluctuates within wide limits.

The callus on young plants of Pisum develops very rapidly in cotyledons of Phaseolus and Vicia, under favorable conditions, it attains a considerable size even a few days after the injury. In cuttings of woody plants, this formation is slower. Sorbus developes abundant callus within the course of the first week; Populus, Salix and many others also react relatively quickly, while months elapse before cuttings of Ostrya show a moderately strong callus ring on the cut surface.

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[1] Sorauer assumes that the "woolly stripes" are produced by excess of water.

[2] Unters. ueb. d. Grenzen d. Teilbarkeit im Pflanzenbreich. Verh. Zool.- Bot. Ges. Wien, 1894, Bd. XLIII. p. 310.

[3] Physiol. Unters. ueber amitotische Kernteilung. Pringsheim's Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 48.

Similar differences exist, in regard to the quality of the callus tissue produced. Populus heads the list of the
(168) many woody plants with cuttings of which I have worked. In moist air masses of tissue often more than one centimeter high and wide grow out on the cut surface. Cuttings of many other woody plants produce only a low callus ring (Ulnus, Salix, Ostrya, Quercus, etc). Further, in Ulmus and Populus, the stimulus proceeding from the place of injury also makes itself felt at a considerable distance from the cut surface. Through abnormal cambial activity, the bark is distended until it may at times even rupture. In most other woody plants abundant cell division takes place only in the immediate vicinity of the place of injury.

We will have to trace these and similar differences in the formation of callus to specific peculiarities of the plant species concerned, when a closer analysis of the causes may not be possible.

As may be surmised, the nutritive condition of the object under investigation will influence the formation of callus. If we compare the organs of one plant which are rich in food stuff with those of the same species poor in food stuff, we find that the former develop wound tissue more abundantly than the latter. The difference between the action of the cotyledons of many Leguminoseae is most striking. (Vicia, Phaseolus, etc.). Rich in proteins and starch, they proliferate the tissue on the cut surface to an extra-ordinary degree, but the thin leaf blades of the same plants develop only weak callus. We find the same difference between cotyledons and foliage leaves of the Cucurbitaceae, (Luffa, Cucumis, etc.) and others. The fact that a more luxuriant callus is formed in injured leaves (cotyledons) in the immediate vicinity of the stronger ribs than between them, may likewise be traced to unequal nutrition. No investigation has yet been made as to whether supplying food stuffs artificially from without, treatment with sugar solution and the like, might promote the callus formation of organs. poor in food stuffs.

Concerning the "external" conditions which may be modified as one wishes in the experiment and their effect studied, the following should be emphasized.

The influence of necessary moisture on the injured tissue is a condition preliminary to every callus formation, whether it be in a liquid or gaseous form; callus may be formed under water as well as in moist air, but not in dry air. Many plants indeed form callus, only in moist air, and the callus formation in all plants is much more abundant in moist air than under water - supposedly because the absorption of oxygen and transpiration are hindered under the latter conditions. Gravity and light are not decisive in the formation, or, rather, the non-formation of the callus. Indeed it developes often more abundantly in cultures in the dark than in the light (for instance, in Populus); perhaps the humidity of the air, increased in the dark, is the cause of this. Of course, there is no formation of chlorophyll in the dark.

If a cutting be left with both ends in moist air, it develops abundant callus on both cut surfaces. If one end is in dry air, which, as previously stated, prevents all callus formations, the callus tissue can develop only on the other end,
(169) where conditions are favorable. If one end is in water or sand, the other in moist air, the latter is then preferred and de-

velops callus. I know of only a few cases in which callus is formed simultaneously on the end under water. A very small "water-callus" is produced in cuttings of Populus pyramidalis, in the formation of which, in my experience, only the cambium participates while bark and pith remain inactive. I found callus produced in Sambucus and Ligustrum under water by the activity of the bark tissue, when the conditions were similar.

If, in the last named case, the cut surface fails to form callus in sand, the arrested respiration and transpiration may indeed be to blame for it. However, callus may be formed in the end in the sand, if the action of the dry air makes its formation impossible at the other end[1]. That portion is therefore preferred for this formation which is at the time under most favorable conditions.

Also, if the formation of callus in cuttings is temporarily arrested by unfavorable conditions, the tissue does not on this account lose the ability to form it. I found callus tissue produced to the usual amount on poplar cuttings, which had lain about four weeks under water, after they had been brought into a moist room. Titmann obtained the same result. He put the cut surface in plaster casts and then, after removal of the plaster bandage, found them developing callus. Titmann calls attention further to the fact that poplar cuttings, with scars left on the main axis by the falling off of dead side branches, form callus on these already healed wound-surfaces through the action of a moist atmosphere. "Therefore the scarred wound acted in this just as a fresh, unscarred one would have done. The results of the injury therefore allow a continuance of conditions, which later make possible the formation of the callus".

Correlations exist further between the formation of callus tissue and the development of side shoots on the cuttings. No case is known to me, in which the production of a callus would have been completely suppressed as the result of an abundant formation of side shoots (favorable conditions being presupposed), but indeed its development is often retarded to the benefit of the side shoots.

In conclusion, still a few words concerning "polarity". An object suitable for the study of this is again offered by the oftnamed poplar cuttings. Even under equal external conditions, the capacity of both cut ends for forming callus is not perfectly equal. If a number of cuttings are placed in water, some upright, some inverted, with the upper cut surfaces favorably arranged for callus formation, it is found that the inverted examples develop a more luxuriant callus than do those normally oriented; the basal poles are capable of a more abundant formation of callus than the apical. I observed the same phenomenon in Rosa. From the observations of other authors, on girdled stems and the like, it takes place also in a number

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[1] Compare also Tittmann, Physiol. Unters. ueb. Callusbildung an Stecklingen holziger Gewächse. Pringsheim's Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 164.

(170) of other plants[1]. In most of the woody plants, whose cuttings I investigated, an obvious difference between basal and apical poles could not be proved. As yet, no case is known to me, in which, the apical end of sprout-cuttings of any certain species, was the one preferred. However, I do not consider it at all impossible that further investigations may make known exceptions of this kind (compare that said below, concerning roots).

In Populus, Rosa and others, polarity may be recognized in the tissues derivatives of the cambium. The question as to whether other kinds of tissue may show the same difference in their callus products deserves still closer investigation. As yet, in the formation of bark callus, I have noticed a preference for the basal pole only in cuttings of Alnus.

Polarity as found in pieces of the stem may also be proved in other organs. Petioles of Populus form a more prolific callus on the pole nearer the place of insertion of the leaves than on the pole toward the leaf blade. Among leaves, the previously mentioned cotyledons of the Cucurbitaceae (Cucumis, Luffa and others) have been proved well adapted for this. If the seed leaves of the young plants are removed, cut across and kept in moist air, they form abundant callus tissue on the wounds of the ribs. The difference between the basal and apical pole is unmistakable at the place of the cross sectioning; the injured surface toward the base forms callus very abundantly, toward the apex very sparsely.

Among roots, I have investigated especially those of the dandelion (<u>Taraxacum officinale</u>) which, as is wellknown, may easily be propagated by root-cuttings[2]. If pieces of roots, 2 to 3 cm. in length, are put into a moist place in such a way that both cut surfaces remain exposed to the air, an effect of polarity is evident in the formation of the callus taking place soon, since almost all pieces of the roots develop callus masses first of all on the basal part, i. e. on the side toward the root neck, while the apical end remains for the present free from callus, and participates only later in its formation. Rechinger (loc. cit.) also proved polarity of the same kind in other kinds of roots. According to his investigations, root cuttings of <u>Medicago sativa</u> form a striking exception, a powerful tuber-like callus is produced on the root end, while the callus on the sprout end remains small.

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[1] De Vries, Ueb. Wundholz. Flora, 1876, Bd. LIX, p. 2. Vöchting, Organbildungen im Pflanzenreich, 1884, Bd. II. Barthelemy, De l'infl. de la tension hydrostatique et de ses variations s. l. mouvement des liquides d. l. veg. etc. Mém. Acad. Sc. Inscr. Bell. Lett. Toulouse, 1881. Müller, N. J. C., Kulturversuche an Weidensteckl. Ber. d. D. Bot. Ges., 1885, Bd. III, p. 159. Kny, Umkehrversuche mit Ampelopsis quinquefolia u. Hedera helix. Ibid., 1889, Bd. VII, p. 201. Tittmann, who worked also with poplar cuttings, seems to have overlooked this polarity. If itis a question in any investigation of obtaining the most luxuriant callus excrescences possible in a short time, it is advisable to place the cuttings upside down. The callus formations described above (compare fig. 60) originate from cuttings inversely oriented.

[2] Compare Wiesner, Elementarstruktur, 1892. p. 112. Rechinger, l oc. cit.

The phenomena here described are most closely connected with the action of unlike external conditions already discussed. The "polarity" expressed in the callus formation of Taraxacum
(171) roots does not rest entirely upon the fact that the apical cut surface was permanently, or at least at the beginning of the experiment, incapable of forming callus. If root cuttings of Taraxacum are inverted and placed in water, in such a way that only the apical poles extend into the air, callus is formed on the latter while the basal surface remains free from it just as when inverted specimens are put in sand, or in plaster, etc. The polarity then seems to be "reversed". Poplar cuttings behave similarly. If they are put in water in a normal position, the basal pole is not only unable to develop a more luxuriant callus, than the apical one but its callus, if developed at all, is less than that of the other pole. If both poles are placed under the same external conditions land one pole nevertheless seems to be preferred, or if only one of the two develops callus, this proved only that the internal conditions, likewise affecting the formation of callus, are unlike at both poles and that, as always, that pole shows the most abundant tissue production, in which exist conditions more favorable for tissue formation. It is difficult to say, what these internal conditions are. I suppose that here, as is so often the case, inequalities in nutritive conditions decide the matter, and I return to the old assumption of a decreased flow of the sap, in order to explain the preference of the basal pole in pieces of the stem, leaves and petioles. Taking this kind of sap current for granted, an accumulation of food substances on the basal pole may well be conceived. Analogously, a stream directed toward the upper end, must be assumed in roots, in order to explain the superior nutrition of the upper end of the cutting.

The processes of tissue differentiation depend also on definite external conditions. We can study the action of arresting factors in abnormal tissues, as in normal ones. It is a matter of course that the cells of the callus roll remain free from chlorophyll, when shut away from light. In Populus the wound tissue remains snow white, in others it assumes a yellowish tone. The fact that I could find no tracheids in the callus of cuttings of Amygdalus, Corylus and Forsythia is undoubtedly connected with the conditions under which the callus was produced (too slight transpiration?). A more exact testing of the question was not undertaken.

It should be noted in conclusion, that callus tissue can be produced in the plant body even in the "normal" process of tissue formation. Such a case occurs if the "mechanical ring" in shoots of many plants is finally broken by continued secondary growth in thickness. The "physiological" wound thus produced is soon closed by an in-growing parenchyma, comparable to callus.

Formation of organs in the callus

In very many woody plants, organs of different kinds are stimulated by injury to the formation of adventitious vegetative points - adventitious shoots and adventitious roots. These,
(172) vegetative points are thereby produced directly from cells of the permanent tissue of the wounded plant organs, or a callus is first formed and from this the vegetative points. Adventitious structures of the first kind exist in many ferns, in the leaves of many monocotyledons etc. Adventitious structures of the second kind in leaf-cuttings of Peperomia, in the shoot-

cuttings of the poplars, elms etc., which usually develop numerous "Lohden wedges" from the callus[1]. Further, there are plants which produce new vegetative points directly from the cells of their permanent tissue as well as by the mediation of callus tissue; for instance, Begonia leaves after removal from the stalk and injury to their ribs, produce new shoots and roots directly from the epidermal cells as well as from the callus tissue, produced on the edge of the injury on the leaf[2]. It has never as yet been observed in higher plants that the cells exposed on the surface of the wound would have been able to produce a new vegetative point, without the interposition of callus tissue.

The consideration of these regenerative processes is only loosely connected with "pathological anatomy", in as much as, in the formation of root or shoot vegetative points, the products of abnormal tissues is stopped by the formation of normal ones. Nevertheless a few remarks concerning the <u>formation of organs in callus</u> may well be added here. The fact that meristematic complexes in the form of shoot or root vegetative points can arise from the cells of the callus tissue[3] is one of its most important characteristics.

Callus occurring on injured roots may be just as capable of forming organs as that on pieces of the stem and on leaves. Yet in most plants not all organs seem to be able to form new vegetative points from their callus; in many others the ability to do this is lacking in the callus of all organs[3], - or perhaps we are ignorant of the conditions under which the callus tissues of these plants may develop vegetative points.

Up to the present the callus tissues of poplar cuttings have been the most carefully investigated as to their ability to form adventitious organs. If they are placed in the usual way in water, in a few weeks a large number of adventitious shoots are developed from the callus. Thus it is shown, that light has no influence on the formation of the latter. Naturally adventitious shoots sprouting the dark have the character of etiolated ones. Further it is shown, that cuttings, of which the apical ends are immersed, form adventitious shoots on the basal poles, which extend into the air. According to Tittmann roots may be produced from the basal poles of poplar cuttings, when placed under water.

The root-pieces of Taraxacum which form callus behave similarly in regard to the formation of shoots. As has been said; when kept in moist air, they form their callus preferably on
(173) the basal pole, (the one toward the root neck). Placed inverted in the water, sand or plaster, the apical pole as well forms callus and adventitious shoots with equal luxuriance. It is indeed possible to cause these pieces of roots which have formed callus and adventitious shoots on the sprouting pole, supplementarily to form a second callus and a second series of

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[1] Further examples of Beverinck. Over het outstaan van knoppen en wortels uit bladen. Nederl. Kruitk. Arch., 2. serie. deel III, p. 438. Rechinger (loc. cit.) and others.

[2] According to Hansen, Vergl. Untersuch. ueber Adventivbild bei Pfl. Abhandl. Senckenberg. Naturf. Ges. 1881, Bd. XII.

[3] In leaves which grow roots after separation from the axis, these roots are very often produced not from the callus, but above the cut surface.

vegetative points by placing them inverted in water, sand or plaster, so that in this way root cuttings can be produced, which develop adventitious shoots on both cut surfaces[1]. The development of new organs, like the formation of callus, takes place at that end which is placed under the more favorable conditions[2]. In Taraxacum the production of roots from callus falls far below the formation of shoots.

The development of adventitious shoots from callus is arrested by the formation of side shoots in the cuttings which carry it; on the other hand, a luxuriant formation of callus often hinders the production of adventitious roots on the cut surface. Sorauer has already referred to this.

The investigation of conditions under which vegetative points are formed in callus and under which shoots, or rather roots, are produced, promises many interesting results. I refer again to Sorauer's statement[3] according to which callus tissues of conifers, Ericas and other plants do not produce roots until after artificial incision.

Wound-wood

Besides a thin walled, homogeneous callus parenchyma, many plants, after injury, produce tissues of other kinds, which become similar to wood tissue through a develpment of tracheal elements. The tissue resembling wood, which is formed after injury, is distinguished from normal xylem by its simple histology. We will term it wound-wood and for this reason add it to the list of kataplasms.

The fact must now be emphasized that tissues of the kind described, resembling wood, are usually produced not only after wounding but also by the action of other injuries. In the present chapter, we will speak not only of the wood formed on the wounditself but also of other tissue products resembling wood, whatever may be the interference to which they owe their
(174) production. Those products will be described in a later section which arise after infection by foreign organisms, - that is "gall-wood".

We described above the case studied by Kny and others, in which young shoots split lengthwise can fill out anew the interrupted cambium ring in both halves by means of callus tissue,

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1 Wiesner (loc. cit.) observed as exceptions some Taraxacum root cuttings, which had formed sprouts on both sides. It would be interesting to follow the further development of such root pieces and to prove whether possibly and in how far the double development of shoots influences their histology. Further literature on Taraxacum in Wakker, Onderzoekingen over Adventive Knoppen. Amsterdam, 1885; Goebel, Ueb. Regeneration in Pflanzenreich. Biol. Cbl., 1902, Bd. XXII, p. 385.

2 In the process of root formation and bud-development in willows, described by Vöchting (loc. cit.) the polar contrast seems to be independent, to a high degree, of external factors, Its reversal has not yet been possible. The same holds good in my opinion for the polar Bryopsis, with which Winkler worked. (Ueber Polarität, Regeneration und Heteromorphose bei Bryopsis, Pringsheim's Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 449.

3 Populäre Pflanzenphysiologie f. Gärtner, 1891, p. 169.

this callus is produced from the pith, bark and cambium of the split shoot and from it a new cambium, which is attached at both sides to the ends of the normal cambium halves (see above p. 20). Similar conditions exist in older branches of woody plants, in which the wood body is exposed by some injury and the thickening ring interrupted. The cambium furnishes the above discussed callus and a new cambium is produced from it, which attaches itself to the normal one. By means of its capacity for division, the roll lying upon the surface of the injury constantly becomes larger, the cambium produces bark tissue on the outside, wood tissue on the inside. This we must term wound-wood because of its structure, since it varies from the normal. All possible transitional stages exist between those cases where the new cambium produces normal (or nearly normal) tracheal elements and those in which it produces typical wound-wood. Just as we found a production of undifferentiated tissue termed callus, not only atthe place of injury itself, but also at a considerable distance from it in the form of a "Lohden wedge" between the wood and bark, so under the influence of increased stimuli an abnormal wood occurs at some distance from the place of injury, near the normal xylem already existing. Although the wood appearing on the wounded surface, by which the exposed places are "covered over", seems to have some especial significance, this seems lacking in the wound-wood of the second kind named. When considering the matter anatomically, we will refer simultaneously to both kinds of wound-wood.

In the literature on this subject, the investigations of de Vries and Mäula come especially under consideration in regard to inquiries concerning life-history and histology[1]. Besides these, references may be made also the statements on life-history in the preceding chapter and the literature there cited.

We will consider first of all those wound-wood tissues which may be produced developmentally by the cambium of wounded shoots and roots.

Histological Composition and Course of the Fibres in Wound-wood

The deviation of the wound-wood from the normal differs according to whether its formation is brought about by cross cuts into the cambium or by longitudinal wounds. The wound wood is characterized in longitudinal wounds by a wide-celled structure and more numerous ducts than under normal conditions. The libriform fibres are less prominent.

(175) The action of cross wounds must be described more in detail.

De Vries proved that in *Caragana arborescens* it was possible to demonstrate the action of wound stimuli on the formation of wound tissue, even at a distance of 9cm. from the wound itself. The deviation of the wound-wood from the normal becomes less, the more distant its formation from the place of injury. The difference is the greatest directly at this place. The cambial cells devide repeatedly as described above, perpendicular to their long axis, thus furnishing only short membered cells as a result of a continuation of their normal tangential activity. The nearer the cambial cells are to the place of

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[1] De Vries, Ueb. Wundholz, Flora, 1876, Bd. LIX, p. 2. Mäule, Faserverlauf im Wundholz. Bibl. Bot., 1895, Heft 33.

injury, the more cross walls are formed. As a result of this, the "short-celled zone" of the wound-wood is produced near the place of injury, at a further distance, transitional forms, which finally pass over into the "long-celled zone" of the wound-wood, which is produced from undivided cambial cells.

The cambial daughter cells of the short celled zone produce, near the edges of the wound, a wound-wood composed of polyhedric parenchymatic cells, whose separate elements generally resemble the cells of the medullary rays in normal wood, only a few becoming parenchymatic tracheids through characteristic thickenings of the walls. At a greater distance from the wounded surface the daughter cells of the cambium are slightly pointed to a spindle form .

In the long-celled zone the cells usually retain the character of wood-parenchyma. Between them narrow vascular cells are produced which are united into cord-like groups; but wood-fibres and broad ducts are lacking.

After the formation of the elements described, which, with de Vries, we may term primary wound-wood, there follows, in the short celled zone as well as in the long celled one, a formation of a secondary wound wood. The cells newly produced gradually assume a normal form, the tissue regains its normal composition. This transition is especially worth noticing in the short celled zone; in which the short membered cambial zone must be gradually replaced by the normal long-celled one. According to de Vries, a few of the short cambial cells grow in length thereby crowding upon the others.

If we reconsider the histological results as a whole, we can prove in all cases, in cross wounds as in longitudinal ones, that the wound wood remains below the normal so fas as any differentiation of tissues is concerned. The libriform fibres are either entirely absent, or are very insignificant, the parenchymatic elements advance into the foreground and indeed so much the further, the more energetically the wound stimulus acts on the cambium. Concomitant with the predominance of parenchymatic elements, full of sap is the fact that wound-wood is less resistent to injuries of various kinds (frost, parasites) than is firm normal wood.

De Vries found typical wood parenchyma in the wound-wood of Caragana arborescence, although it is entirely absent in
(176) the normal wood of this plant[1]. Still more striking is the formation of abnormal resin ducts in wound-wood. De Vries found that they are often more numerous in wound wood than in normal wood, and Vöchting[2] proved for Picea excelsa that, reckoned on the surface content, seven times as many occur in wound wood as in normal wood. In fact resin ducts occur abundantly in plants which normally do not develop them, for in-

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[1] That the elements in question illustrate "real" wood-parenchyma "and have not been produced possibly by cross-divisions which had already taken place in the cambial cells, follows on the one hand from the direct observation of the cambium, which lacks divisions at this height", -the long-celled zone of the wound-wood is here concerned,- "and then from the observation, that in exactly radial sections an undivided compensating fibre frequently lies on the outer side of such a parenchymatic fibre". (De Vries, loc. cit. p. 24).

[2] Ueber Transplantationen am Pflanzenkörper, 1892, p. 139, 140.

stance, in Abies cephalonica, which Mäule (loc. cit. p. 18) investigated thoroughly[1].

Wound wood does not always appear as stratified tissues to be considered as a direct continuation of the normal wood. In the cambial callus of cuttings, which swells out over the place of injury, separate cells often assume the character of parenchymatic tracheids as described above. In the production of these we may recognize the beginning of the formation of wound-wood. Not infrequently, tracheid-like cells lie in the callus, united into ball-like groups. In both cases the abnormal tracheal elements remain separated from the normal wood. In the further course of development independent cambial, or meristematic tissues are formed in the periphery of the tracheid groups, through whose capacity for division these groups may be greatly enlarged. The new abnormal cambial tissues can also remain permanently separated from the normal cambial ring.

In spite of the universal similarity in the structure of wound wood in different plants, differences may also be proved in the individual species. Besides the different quantative proportions between tracheid-like elements and those resembling medullary ray parenchyma, besides the formation of the resin ducts already mentioned, etc., the irregular, waved course of the fibres of wound wood elements comes under consideration and has been clearly recognized in macroscopic investigation.
(177) As is already known, the structural appearance, conditioned by the irregular course of the fibres, has been termed gnarled

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[1] It is well to observe here that these abnormal resin containers do not exhibit the structure of normal resin ducts in conifers; "in particular, the epithelial cells lining the ducts are lacking in these. The longitudinal course of the single resin containers was always parallel to the course of the wood fibre;- besides, this course was often interrupted by a bridge, several cells wide, of parenchymatic elements, so that there was not present an actual resin duct, but a continuous row of resin containers, the length of which exceeded three or four times the width". In addition to this, many circumstances point to the fact, "that they do not serve for the continued secretion of resin, but only as store rooms for resin, which was formed in the wound callus, the transference of which to the bark has become impossible on account of the wood mantle lying on this". (Mäula, loc. cit. p. 18, 19. Compare also the further statements on abnormal formation of resin ducts in the discussion of gall-wood). Just because the formation of the characteristic epithelium is not present in the abnormal resin containers and because we are concerned in them only with "ordinary" parenchyma cells, which have been filled with resin, every reason is lacking for seeking new kinds of differentiation processes in the occurrence of the abnormal resin ducts, as will be observed in prosoplasmas. The same holds good for the wood parenchyma cells, which de Vries found in the wound wood of Caragana.

wood (veined or grained)[1].

It may be seen from microscopic investigation, that definite groupings are regularly repeated in the irregular course of the fibres. In vertical longitudinal sections, especially if the wound wood has already attained some size, fibres appear which have been cut slantingly and crosswise. "Just as the elements already produced may vary in length, considerable disturbance in their normal perpendicular course is found which always beginning at the edge of the callus, spreads upward and downward". (Mäula). Among many irregularities the frequent
(178) recurrence of V-, C-, or W- like twisted cells is very noticeable. These are united into groups like balls of thread, (compare fig. 69) as well as context for fig. 102). All elements of wound wood can participate in the construction of these balls. In those pictured in figure 69, taken from the wound wood of Abies cephalonica, parenchyma cells as well as tracheids are found. Tracheids always play the chief role. As Mäula has proved, the wound wood of different plants is characterized by the different size and the different distribution of its ball-formations. Figure 70 throws light on the form of the separate cells which compose these balls. It represents a few strikingly twisted tracheids, here and there branched, from the wound wood of Cydonia japonica. The middle one of the three contains a spiral band. Besides the slender tracheids, short, barrel-like ones are produced and parenchymatic elements often of wonderfully inflated branched forms. According to Vöchting (loc. cit. p. 136) similar forms are found also in the abnormal bark formed after injury, which we can term "wound-bark". In this occurs also the formation of balls as in wound-wood (Cydonia japonica).

Vöchting (loc. cit. p. 132) described this ball-like arrangement of the wood-elements in the wound wood of Cydonia japonica, which was formed in grafting experiments in which the bark rings were inserted upside down. These and other abnormal tissue formations after grafting on Beta vulgaris and other objects led Vöchting to the assumption that "the individual elements of the long axis are constructed with a polar relation, and that their poles are drawn together or pushed away according to whether we bring the unlike or the like into con-

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[1] The formation of gnarls occurs not only after injury, but also in abnormal tissues of other origin. We will have to speak repeatedly of "gnarl tubers" and gnarl structure. Compare also Frank, Krankh. d. Pfl., 2. Aufl., 1895, Bd. I, pp. 80 ff. At this point I would like to call attention casually to the fact that an irregular course of the fibres can even occur where there is no question whatever of hyperplastic formation of tissue. R. Hartig has proved recently, that the "waved or grained structure" in trees is often to be traced back to the longitudinal pressure, "which a side root, growing much thicker towards the top, exerts on the bark and cambium of the lower end of the trunk, or which the branch, in becoming thicker, exerts above and below on the bark of the tree. This longitudinal pressure causes foldings in the bark of thin barked trees, and in the wood produced from the cambium. These run in a longitudinal directions. In trees with thick bark (oak, chestnut, black-alder), on account of longitudinal pressure, the elements of the inner bark and of the wood are wound in wavy-lines, running tangentially. In conifers, waved wood occurs rarely in the trunk". (Holzuntersuch., Altes und Neuws, 1901, p. 52, Ueber die Ursachen d. Wimmerwunchses (Wellenholzes) der Bäume. Cbl. f. ges. Forstwesen, 1901, April).

tact", (loc. cit. p. 151). With the help of these data
(179) on the polarity of cells, Mäula has tried to explain those balled formations which occur so abundantly in wound wood without any previous grafting. Although Mäule's attempt at explanation does not seem to me exactly convincing nor tenable without many auxiliary hypotheses, I will nowlet him speak for himself.-

Mäula starts with the supposition that in new formations of different kinds,- even in wound wood,- the development of the separate elements is unequal, since some are formed early, others are retarded in development. Fibres, pushing forward, will not be able to maintain their struggle to stretch downwards since the callus of the girdling wound here concerned is closed on the under side. The fibres will therefore have to bend. According to Mäule, the fact, that most fibres are bent tangentially along the upper surface of the body of the wound and not radially, may be explained on similar grounds (resistance of the wood). Accordingly, the rootpole of fibre in the adjacent diagram (fig. 71) at first grows out approximately horizontally. "If the resistance also becomes too powerful in this direction there results a further bending downward, if possible; if not, then upward. Thereby its rootpole W1 pushes directly on the rootpole of W2 of another fibre, which may possibly have been somewhat retarded in growth. As a result of this direct contact of two homologous poles, W_2 is obliged to deviate, either towards the outside (left) (as in the figure) or towards the inside (right). There W_2 is pushed along on fibre 1, until any further extension is impossible, or the growth in length of this fibre 2 is ended. The next fibre 3 then pushes on W_2 with its rootpole W_3 and must also bend, carrying its rootpole end along fibre 2.--- It is evident that the fibres 6, 8. etc., which at last are entirely inclosed, have only a very small space for their extension and that finally, necessitated thereto by the pressure of surrounding fibres, two homologous poles can come exactly together. This, however, does not in any way contradict the polarity of the cells. It is only that the power here forcing the ends apart is less strong than the external pressure, even homologous poles of two rod magnets can be brought together, if the free nobility of the rods is prevented".

Tracheid-guares on balls resembling in all essential points those balls described above, are to be found not only within the wound wood formed by the natural cambium, or by newly formed cambial layers but also isolated from these, in the undifferentiated callus tissue. In the luxuriant cambial callus of poplar cuttings, ball-like tracheid groups are produced here and there, as already described. In these, as in those described earlier, we find irregular forms. The root too may be able to produce the same forms of wound wood, as are produced on acillary parts. The same "balls" may be found in the callus of roots as in that of organs above ground. I investigated more closely the callus products of Taraxacum roots. In the basal callus rolls of the cuttings, woody cores are produced composed of long and short tracheal elements. The cells, how-
(180) ever, are differently arranged and in such a way that in every section one meets here and there with groups of cells, cut lengthwise, and side by side others cut crosswise or slantingly. In the middle lie the strongly bent tracheids, such as described above. Round about this woody core there lies a ball-like cambial covering, which on the outside produces con-

centrically layered bark tissue with abundant latex tubes. The separate balls are usually connected with one another and with the cambium of the cutting by means of cambial bridges.

The cases here described prove at the samt time that the formation of the balls is not connected with advanced stages in the production of wound wood, but may also indicate the beginning of its formation.

Tissues furnishing wound-wood

Just as the cambium, to the derivations of which the preceding statements chiefly refer, can produce wound wood or products similar to it, all other tissues, furnishing callus, can also produce wound wood under certain circumstances. The pith is concerned here more than all other tissues. In different plants, for instance in Populus, it is highly capable of forming callus. In the medullary callus, tracheids and groups of tracheids are also produced very early, on the periphery of which are formed new meristematic tissues. The formation of tracheal elements which Prillieux[1] studied in the pith of different cuttings (Coleus, Ageratum, Achytanthus and others) should be mentioned.

A case described by Mäule (loc. cit. p. 27) is of interest for several reasons. In Evonymus europaea, cambial formation was brought about in the pith when it had not been directly injured. In several branches, from which rectangular pieces of the bark had been cut the cells of the round tissue, resembling parenchyma and containing chlorophyll, which lies between the pith zone and the pith, was incited to division beneath the place of injury. From the new tissue thus produced, a cambium was differentiated which, extending like an arch, produced xylem on the inside, phloem on the outside, also a new bark zone and a new cork layer, "so that therefore, all the zones of a regular woody-trunk are formed within the old woody body". "It must still be noted that the beginning of the formation of wound-wood in the pith did not coincide with the beginning of its formation on the external, directly injured, part of the branch. As a result of the exposure, the wood under the places where the pieces of bark has been removed, began to turn yellow, i. e. to be changed chemically. This change progressed slowly towards the center, especially along the medullary ray until the entire old wood body had been altered as far as the injury extended. If the transformation in the medullary rays had penetrated as far as the pith, cell division then began in the latter. There existed here therefore the remarkable case, that the pith was not directly brought to the formation of wound-wood by the injury, not even by the wound stimuli, but only by a secondary phenomenon connected with the injury". We will later find other cases,
(181) which make it seem probable that living elements adjacent to the dead cells can be stimulated to division by the products of decomposition in the latter.

The isolated wood bodies, which Vöchting and others[1]

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[1] S. l. formations ligneuses qui se produisent d. la moelle d. boutures. C. R. Acad. Sc., Paris, 1882, T. XCII, p. 1479.

[2] Vöchting, loc. cit. p. 141, 142. Tschirch, Pflanzenanatomie, p. 396. Mäule, Der Faserverlauf im Wundholz. Bibl. Bot., 1895, Heft. 33, p. 23.

found occurring in processes of cicatrization and coalescence in the bark, seem to correspond in all essential points with the tracheid groups described above. In them also an independent cambium is formed around the core of the wood. The ability to form this kind of isolated wood-cores of larger or smaller compass might well be peculiar to very many, or indeed to all plants which form wound-wood.

Tissues resembling wound-wood are produced also in the callus developed from the ground tissue of injured leaves. At any rate, so far as my experience goes, it must generally end with the formation of isolated parenchymatic tracheids in them. More extensive quantities of tracheal elements occur for example in the form of isolated spherical groups of cells in the callus of detached Vicia cotyledons. Here too we find again the formation of gnarls of moderate size.

Outer Form and Period of Development of Wound-Wood.

Conditions of its Formation.

Wound-wood has no definite outer form. Its form is determined in the first place by the swollen rolls occurring on the surface of the wound, the form of which depends naturally on the nature of the injury. Thus a differently formed wound-wood body is produced after cross or longitudinal sectioning than from girdling or spiral wounds and the like. The wound-wood body always adjusts its form to the space conditions granted it. Therefore it is immaterial for our consideration, whether the cambium is incited to the formation of these rolls by injury, by accidental or intentional mechanical interference with its integrity, or forms them after local injury from frost. If the frost causes the death of the cambium in places of any indefinite extent and if the dead place is later surrounded by rolls of wound-wood, then we speak of canker (frost canker). If the so-called frost tears are caused by a splitting of the wood, the masses of wound-wood produced by their healing are called frost ridges. The manuals of phytopathology give more exact information concerning the significance and distribution of these phenomena[1].

R. Hoffman[2] has shown how the course of the medullary rays in the covering rolls is determined by mechanical incidents.

The period of development of wound-wood varies with conditions and within wide limits, as does that of callus. It is known that the rolls of "canker" (frost canker) are destroyed every winter by the action of cold because of the greater delicacy of their tissues, so that in the following year the injured tree "tries" to heal its wounds by a new overgrowth.
(182) Under these conditions wound-wood can be formed for many years, the rolls of which are laid one above the other like terraces.

The conditions necessary for the formation of wound wood require still closer investigation, as do those of callus formation. As stated above, there has been as yet no successful analysis of the "wound-stimuli" effective here. The dependence

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[1] Compare for example, Frank, Krankh. d. Pfl., 2. Aufl. Bd. 1, p. 207 ff.

[2] Untersuch. üb. d. Wirkung mechanischer Kräfte auf die Teilung, Anordnung und Ausbildung der Zellen etc. Dissertation Berlin, 1885.

upon external conditions of wound-wood formation and of its histology has likewise not been closely tested. Undoubtedly the structure will be influenced by nutritive and transpiratory conditions, as is that of normal tissues. Compare also the statements on callus page 171.

The fact that the conditions giving rise to the formation of wound-wood are not only effective, directly at the place of injury and in its immediate vicinity, but also at a considerable distance is of great importance. De Vries' experiments on Salix, Acer, Evonymus and others (loc. cit. p. 113) prove that, when the outer bark layers are wounded, no wound stimuli are produced, which would cause the production of wound-wood.

Tissues resembling Wound-wood.

Aside from the different forms of gall-wood, to which we will return later, there are abnormal wood tissues which do not arise after injury but from the action of some other factors. These, however, are more or less similar to wound-wood so far as their histology is concerned. Besides these, tissues of the same composition must be considered in the following, concerning which no decision has been reached as to whether their production is due to wound or to other stimuli. We will devote a few lines here to their discussion.

The production of tissues resembling wound-wood proceeds, as does that of wound-wood itself, either from the normal cambium ring or from newly formed, independent cambium.

Abnormal tissues should be considered first of all, which are produced by the activity of division in the normal cambium ring. In all cases, the deviation from normal histological conditions consists in a lesser histological differentiation of the wood tissue produced. The deviations described above are approximated first of all when the parenchyma of the medullary ray increases in places at the expense of the other formal elements of the wood. Abnormally broadened medullary rays are not infrequently found in fasciated branches. The factors, leading to the fasciation and thereby to the change in histology here named, are still unknown. The occurrence of abnormally broadened medullary rays in non-fasciated branches is also not unusual[1].

In other cases normal differentiation is lost to the
(183) secondary woody-coalescence in all its parts. As Sorauer assumes[2], slightly differentiated wood is produced, for instance, in the fruit spikes of Pirus communis, as a result of rich nutrition and abundant supplying of water, and as a sign of the "weakening of the branches through cultivation". Instead of libriform fibres, predominantly parenchymatic elements are produced in the wood and generally remain unlignified. Besides these, a luxuriant development of the bark takes place, which causes it to rupture here and there. Undifferentiated wood is produced also in the "dropsical"

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[1] Sorauer, (Sorauer), Krebsartige Rindenhypertrophie. Zeitschr. f. Pflanzenkrankh., 1898, Bd. VIII, p. 220) traces a case observed on Rosa suppositionally back to too rich nutrition.

[2] Nachweis der Verweichlichung d. Zweige uns. Obstbäume durch d. Kultur. Zeitschr. f. Pflanzenkrankh., 1892, Bd. II, p. 66.

branches of Ribes[1], treated of earlier. Still more examples of this kind might be cited; an arrestment of the processes of differentiation and an increase of the parenchyma contained in the wood is almost always associated with over production of wood.

Those cases must still be mentioned in which new cambial layers are produced, leading to an abnormal formation of wood. Just as in wound tissues described above, isolated wood cores of varying size are produced by the activity of their division.

Sorauer has given thorough anatomical descriptions of the "tuber-like gnarls" of the stone-fruit trees, and Krick of similar formations in beech bark[2].

Sorauer found tuber-like woody bodies in the bark of Pirus malus. In their centres lay one or two hard bast bundles, separated by lignified parenchyma. About these "are layered in a ray-like arrangement, first of all approximately iso-diametric cells of wood parenchyma, lying bluntly upon one another, and usually contraining starch". Little by little this zone passes over into narrowef, thicker-walled wood parenchyma cells, already somewhat elongated and running horizontally or diagonallyp between them are scattered short, broad simple pitted duct cells. These groups have already been divided into numerous circles of bundles by approximately cubical medullary ray cells, lying possibly from 1 to 3 rows thick. The further the cell elements are separated from the centrum, the more marked is the difference between the parenchyma of the medullary rays and the elongated fibro-vascular tissue. Near the centrum, begins also the phenomenon which makes itself felt throughout the whole wood body, that is divided into different annual rings,- viz., that the elements of the fasciated partlying between two medullary rays show a different course than do those of the parts lying near it. While the razor cuts through the cells and ducts of one bundle almost in cross section, it strikes those of the adjacent bundle longitudinally". Many tuber-like gnarls vary from these here described, in that the hard bast bundle is lacking as a centrum; instead of this is found a group of bark parenchyma cells.

The isolated wood bodies which Sorauer (loc. cit. p. 185) found in a branch of Pirus communis resemble in all essential points those described, - in which a one-sided flat swelling was conspicuous. "The cross-section through the middle of the
(184) swelling showed new, isolated, wood bodies almost touching one another, however, at the sides, which were entirely separated from the central wood cylinder of the branch by a normal cambium and secondary bark zone. Each of these wood bundles bore in the center a hard bast group and had also the structure of the centrum of the tuber-like gnarl of the apple, only, the wood cells and ducts were not arranged cone-like on all sides about the centrum but extended parallel to the length of the branch. There were, therefore, no wood tubers, but short wood-cords, which traced further downwards became steadily

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[1] Sorauer, Wassersucht bei Ribes aureum. Freihoff(s Deutsche Gartenzeitung, 1880.

[2] Sorauer, Die Knollenmaser der Kernobstbäume, Landwirtsch. Versuchsstat., 1879, Bd. XXIX, p. 173, Handb. d. Pflanzenkrankh., 2. Aufl., 1886, Bd. 1, p. 726. Krick, Ueb. d. Rindenknollen d. Rotbuche. Bibl. Bot., 1891, Heft 25.

thinner until they showed a simple, weak, ring-like bast circumvallation, formed of lignified parenchyma". Toward the top, the cords approached the central wood-body more and more closely and were finally united with it.

The conditions under which tuber-like gnarls are produced are not yet sufficiently understood. Sorauer states that they are formed "readily near the outgrowing wounded surface"; which argues in favor of the supposition that some of the conditions created by the injury become the cause of this formation.

The isolated woody kernels of tissue which lie in the bark of Fagus silvatica (fig. 72) and which have been thoroughly described by Krick as "bark tubers", show a still greater diversity in development and histology. They are either produced in connection with preventitious buds or short shoots which have been separated from the wood body of the mother stem,- their cambium thus being descended ontogenetically from the normal cambium ring, in as much as it was connected with it, at least at the beginning, or they are independently formed of buds and short shoots without having any connection with the mother stem. In the later case, Krick distinguished between tubers with central wood bodies and those which enclose cork tissue at their centre. The formation of these bark tubers seems to have nothing to do with any injury and its results.

Krick has collected the statements of earlier authors concerning bark tissues (loc. cit). As one of the most important works may be named here that by Gernet[1].

(185) The gnarl-tubers of different Eucalyptus types, already repeatedly studied, are of especial interest. They occur in the axes of the first pairs of leaves and, according to Jönsson[2], are produced under the influence of unfavorable nutritive conditions. The dependence of their growth upon that of the whole plant reminds one of the correlation heteroplasmas mentioned above. Jonsson could bring about the production of gnarl-tubers by cutting off leaves, buds, or branches, i. e., he could hasten their growth. According to Vuillemin, the Eucalyptus tubers are produced under the influence of a parasite, Ustilago Vrieseana, which is said to cause tuber-like new formations of other Myrtaceae (Myrtus, Acmena, Tristania, Melaleuca, Callistemon)[3,4].

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1 Ueb. d. Rindenknollen von Sorbus aucuparia. Moskau, 1860.

2 Ytterligare bidrag till kannendomen om masurbildningarna hos Myrtacerna, sörskildt hos slägtet Eucalyptus. Bot. Not., 1901, p. 181, further bibliographical citations there in.

3 Vuillemin, S. l. tumeurs ligneuses prod. p. une Ustilaginée Chez. l. Eucalyptus. C. R. Acad. Sc. Paris, 1894, T. CXVIII, p. 933. Les broussins dd Myrtacées, Ann. Sc. agron. Franc. et étrang., T. II; compare Zeitschr. f. Pflanzenkrankh. 1896, Bd. IV, p. 167/

4 Further data on gnarl formation may be fouhd also in Andreae: Abnorme Wurzelanschwellungen bei Allanthus glandulosa, 1894, v. Kolb. Abnorme Wurzelschwell. bei Cupressus sepervirens; Arcularius, Fall v. Wurzelkropf bei Abies Pichta, etc. 1897 (Erlanger Dissertations).

The "Chichi" (Nipples) of Ginkgo biloba are gnarl formations which arise after injury but originate like many bark tubers of the beech from definite buds. They are leafless, branch-like excrescences which, on the shoots and roots, can grow out into adventitious buds, even becoming 2 meters long. Keniiro[1] calls them "cylinder-gnarls" on account of their form. The arrangement of their tracheids is irregular, like gnarls.

4. Wound-cork.

After injury of different organs,- roots, tubers, rhizomes, stalks, leaves, inflorescences,- several layers of cells are often formed arranged in rows, and generally in immediate adjacency to the place of injury. Since the newly produced walls react to known reagents (sulphuric acid, chlor-iodid of zink, Sudan III, etc.) as do those of cork, since the abnormal tissue corresponds to cork in the arrangement of its elements and since further the dependence of its production upon the abnormal conditions created by the injury is unmistakably, the products described have for a long time been called wound-cork.

Wound-cork is generally formed on all parts of the wound and at its edges connects directly with the normal membrane of the injured plant organs,- epidermis or cork. The new cork formation thus seems to close the wound. Since wound-cork doubtless reduces the transpiration of the exposed tissues and may indeed in other respects be able to compensate for the normal membrane, we may assume that, by its for-
(186) mation, the continuance of the exposed tissues and of their functional activity is assured and we may speak of a healing of the wound by the formation of cork.

There is not much to be said concerning the life-history of wound-cork. A number of celldivisions takes place in either one or in more cell layers under the surface of the wound and parallel to it. Not infrequently an obvious meristen zone is thus produced and the wound cork is increased through the activity of its division. The ground tissue is here, as in many other cases, by far the most efficient; the thin-walled, parenchymatic parts as well as the collenchyma fibres are capable of producing wound cork. Besides these, the cambium and the bark produced from it come under consideration and finally the epidermis also. If the last becomes active in the formation of wound cork, each cell generally seems to be capable of very few divisions. In wounds on the stems and leaves, the derivation of the epidermis and of the ground tissue form together a homogeneous wound cork plate.- It is known that the place of production of the normal cork of the trunk (epidermis or ground tissue) is, however, usually constant in genera and families.

The histology of wound cork is characterized by the arrangement in rows of its sheet-like elements. The walls of wound cork are always thin and often folded. I found thin walled wound cork even in Cytisus, the normal cork of whose trunk is known tobe made up of thick walled cells. Differentiations of any kine whatever, formations of zones, lenticels and the like, entirely absent in wound cork. Its cells are

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[1] On the nature and origin of so-called "chichi" (nipple) of Ginkgo biloba. Botan. Magaz. 1896, Vol. IX, auch Zeitschr. f. Pfl. Krankh. 1896, Bd. VI, p. 225.

usually larger than those of the phelloderm. It is worth noticing that even those plants can be capable of forming wound cork which, under normal conditions, develop no cork on their stalks. (Experiments on Viscum)[1].

Nearly related to wound cork is the multicellular tissue, which often grows out from the wounded bark on the places of insertion of roots and buds. If, for example, Salix branches are placed in water or brought into a room saturated with water vapor, numerous roots develop on them, at the base of which a small, porous, whitish mound of tissue is noticeable, which has the greatest similarity to outgrowing lenticels. (Compare p. 75). It is founf in cross-section that a meristem is produced near the wound in the bark, the derivatives of which resemble elongated colorless balls or scas. Between the individual cells, which are often entirely detached from one another, lie large intercellular spaces filled with air. Therefore the structures described also histologically resemble hypertrophied lenticels. Mohl[2] has called attention to this similarity and warned others against confounding the forms. The same tissues are also produced as in the places of insertion of the roots, if buds injure the tissues of the bark during their development. (Fig. 73). The walls of the wound tissue described do not become cork.

As far as the <u>conditions</u> are concerned, under which wound cork is produced, the relation of its formation to the
(187) injury and to the conditions created by it, first come under consideration. Each break in the continuity of the tissue can cause the formation of wound cork, no matter if the wound lies on the upper surface, whereby the surrounding air has direct access to it, or if "internal" injures are involved such as are produced perhaps by twistings of stalks, etc.[3]. A preliminary condition of its production, however, is that at least a small degree of transpiration must be possible for the exposed tissue. On this account no wound cork can be produced in the sting canals made by parasites which produce galls, but only callus tissue (hypertrophy and hyperplasia). In the succulent, juicy gall of <u>Nematus vallismerii</u> upon whose innermost tissue voracious inhabitants of the gall cavity constantly graze, a richly outgrowing callus is produced, but wound-cork only in exceptional cases (in injured galls). Tissues which seem incapable of forming callus, such as the parenchyma of the potato tuber, develop wound-cork after injury, only when transpiration is possible. There is no formation of the wound-cork under water[4]. Of the many changes in conditions usually caused by injury, apparently the abnormally

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[1] Damm, Ueb. d. Bau d. Entwickelungsgeschichte u. d. mechan. Eigensch. mehrjärh. Epidermen beimd. Dikotyl. Beih. z. Bot. Cbl., 1901, Bd. XI, p. 219.

[2] Quoted above p. 75, note 1.

[3] Compare v. Brefeld, Ueb. Vernarbung u. Blattfall. Pringsheim's Jahrb. f. wiss. Bot., Bd. XII, p. 133, also above p. 162, note 2.

[4] On the causes of the formation of wound cork, compare also Frank, Krankh. d. Pfl. 2 Aufl., Bd. I, p. 61 ff. Kny, Ueb. d. Einfl. v. Druck u. Zug auf die Richtung der Scheidewande u. s. w. Ber. d. D. Bot. Ges., 1896, Bd. XIV, p. 378.

increased elimination of water from the exposed cells and tissues comes first of all under consideration in the formation of wound cork. It is certain that "wound-cork" can also be produced independently of any injury, if only the elimination of water is in some way abnormally increased. A case
(188) of this kine seems to me to be present when the large celled, thin walled, strongly transpiring intumescences of Hibiscus are separated from the normal mother structure by a layer of wound cork[1]. It is well known that wound-cork is formed sooner or later in callus excrescences, which grow out on the cut surfaces of cuttings etc. It is difficult to decide whether the formation of wound-cork should be considered as a delayed effect of wound-stimuli, or as a result of the strong transpiration, to which the callus tissue is exposed. Similar conditions are present in the intumescences shown above (fig. 23), the formation of which is preceded by a dissolution of the normal cell-continuity and the foundation of which is often connected directly with wound-cork. In these, as in callus, it does not seem to me improbable that the abnormally increased transpiration of abnormal tissues can call forth the formation of wound-cork entirely independently of the dissolution of the tissue continuity and of "wound-stimuli"[2].

Up to the present, it has not been proved definitely that under certain circumstances factors other than abnormally increased transpiration can also cause the formation of wound-cork; but there is much in favor of it. Wound cork is often produced when separate cells or cell-groups die in the inner part of the tissue; a more or less strong cork mantle is formed around this center of disease. It does not seem to me very probable that the transpiration of the cells left in the center of the tissue has been abnormally increased, and that the formation of wound-cork has been caused by this; rather we should not reject the supposition that some products of disintegration, produced at the center of disease, have incited the adjacent healthy tissue to the formation of cork. One of Vöchting's[3] observations favors this. He often found dead pieces of tissue enclosed in the

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[1] Compare above p. 86 note.

[2] The production of cork in the leaves of Ribes grossularia seems to be comparable with the cases named. In a low lying part of his experimental garden, Sorauer (Handb. d. Pflanzenkrankh., 2. Aufl., 1886, Bd. 1, p.222) observed gooseberry bushes with groups of branches entirely gray leaved. Sorauer designates the disease as cork-sickness. The individual leaves were either covered only with two cushions or cork, spread out like wings, or were coated over and over with cork. I think it allowable to deduce from Sorauer's statements concerning this disease, which I myself have had no time to investigate, that the formation of distended intumescences precedes the abnormal production of cork - the palisade cells stretch and burst the epidermis - then follows the formation of wound cork.

[3] Ueber Transplantation am Pflanzenkörper, 1892, pp. 113 ff. The cells connecting directly with the destroyed parts always become cork; "those following next, however, often the majority present, are still unbrowned and of a cellulose nature. This is then retained even if all processes of growth have long ceased". The turning to cork is almost always absent, even "if thickened walls turn brown in the zone of contact and delicate walls occur in the elements belonging to or adjacent to these". If is an open question whether these cells also can serve for a covering

cicatrizations of the beets upon which he operated; but cork had been formed only in the vicinity of those enclosures which had turned brown, in which therefore some products of disintegration had been produced. In different succulents which showed an especial "tendency" toward a vigorous formation of
(189) wound-cork after injury, I repeatedly observed strongly developed formations of cork in the region of dead parts of tissue, and, as I suppose, under the influence of unknown chemical combinations. In this connection belong perhaps the "cork excrescences" studied by Bachmann[1], which make possible the production of extensive tissue protuberences or which in places can channel the organ concerned or completely perforate it, (Ilex, Zamia, Ruscus etc.) while division of the parenchyma cells and the suberization of their products of division progresses further and further into the interior of the leaf. Histologically and ontogenetically the cork excrescences described and illustrated by Bachmann correspond throughout with typical wound cork.

The manuals of phytopathology should be consulted on potato scurf or scab. Nöbbe produced cork excrescences on potato tubers by cultivating them in water[2].

Like callus (see above), wound cork can be produced also on "physiological" wounds. Many plants develop it, for example, on their leaf scars[3].

5. Galls

We have termed gall-formations all abnormal tissues produced by the action of vegetable or animal parasites. The great majority of these arise either through cell growth alone (gall-hypertrophy) or through cell division (gall-hyperplasia): Since, in the latter case, the newly produced tissues differ more or less strikingly from normal ones, we are concerned only with hyteroplasms in such gall-formations.

The number of heteroplastically constructed galls is extraordinarily large; even the diverse gall hypertrophies re-

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[1] Ueb. Korkwucherungen auf Blättern. Pringsheim's Jahrb. f. wiss. Bot., Bd. XII, p. 191.

[2] Die Kartoffel als Wasserpflanze. Landwirtsch. Versuche-Stat., 1864, Bd. VI, p. 57.

[3] Compare further Tison, Rech. s. la chute d. feuilles d. Dicotyl. These, Caen, 1900. This tissue becomes of interest for pathological plant anatomy only when it arises at the wrong time as a result of abnormal conditions. I would like to refer at this opportunity to the fact that the "tissue of separation", which makes possible the freeing of the leaf from the axis, is produced prematurely if the leaves are robbed of their blades; the axis then lets the petioles fall off. The question whether the results of wound stimuli are to be recognized in this needs supplementary testing; it is more probable that the reduced transpiration determines it; also branches left in moist air are known to drop their leaves. (Wiesner, Untersuch. über die herbstliche Entlaubung d. Holzgew. Sitzungsber. Akad. Wiss. Wien, 1871, Bd. LXIV). In these and similar cases, the wound produced by the fall of the leaf is no longer a "physiological" one. The question as to whether the tissue of separation produced on mutilated leaves and by action of moist air corresponds with the normal one, needs supplementary testing.

main far below these in number. Heteroplastic gall formations occur in very different kinds of plants, appear on all plant organs and may be traced developmentally to very different normal tissue-forms. A few general notes might be in order before we proceed to a description of the different fall forms.

(190) One generally terms galls, or Cecidia[1], those variations in form which are caused by foreign organisms. Thomas, whose definition of the conception of the gall has received the most approval, explains as a gall, "every variation in the form of plants which is caused by a parasite", and adds: "in this explanation the word formation is to be taken directly in the sense of the process (therefore active), not merely in the sense of its result. Each leaf eaten or mined by caterpillars shows a formal variation. No one will associate such changes with cecidia. To the nature of these latter belongs active participation of the plant, its reaction against the stimulus then experienced"[2].

I have attempted at an earlier opportunity[3] to define more sharply the definition given by Thomas and have advised a closer consideration of the biological connection between the plant bearing the gall and the foreign organism producing it, in the formulation of the definition. Clearly there are a number of variations of form which are caused by stimuli given by the foreign organism and in which abnormal tissues are produced, without one's venturing to call them galls. Such a case is met with perhaps when a "mining path" is filled with callus (examples above p. 163). No one will contend that such cases present gall-formations. The abnormal tissues show no connection with the foreign organism,- aside from an etiological one. In our opinion one essential of a gall is that the abnormal parts of the plant affected bring about symbiotic relationship between these and the parasites producing the gall. These symbiotic relations are primarily of a nutritive physiological nature; the abnormal tissues furnish food for the parasites. Additional relations exist since the host plant not only furnishes sufficient maintenance, but also as good shelter. The galls are thus formal variations of the plant which promote the development of the parasites and are in this sense "expedient" for them. Now, since according to the above symbiosis with the producer of the gall always signifies a loss of nutritive material for the host organism, the part which bears the gall often dies a premature death and further, since in all cases as yet known the parasite producing the gall performs in return no service to the host, as one is often inclined to assume in so-called mutualistic symbiosis, we are concerned in cecidia with formal variations which are injurious to the development of the organism bearing the gall.

Of all the variations in form satisfying the demands of our definition, we will naturally treat in the following only those in which abnormal tissues are produced. To present the doubling

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[1] Thomas, (Zur Kenntnis der Milbengallen und Gallmilben etc. Zeitsch. f. ges. Naturw., 1873, Bd. XLII, p. 513) has introduced this word (derived from Knxls). Compare also the critical remarks by Trotter, Studi cecidiologici II (Nuovo giorn. bot. ital., 1901 N. S. Vol. VIII, p. 557).

[2] Loc. cit. p. 513, 514.

[3] Küster, Ueber einige wichtige Fragen der pathol. Pflanzenanat. Biolog. Centrabl., 1900, Bd. XX, p. 529.

(191) of infloresences, caused by gall-insects and gall-plants, a turning green of tissue any abnormal branching etc. is the task of the morphologist.

Galls form a group, well defined etiologically and biologically. In their histology, however, we will find scarcely one feature, which is common to all. Even when considering only gall-hyperplasias we will find no common characteristics,- except that a production of heteroplastic tissue is involved in all. This is either extraordinarily simple histologically, showing little or no differentiation, and as a result, the same characteristics as met with in "arrested developments"- or specific differentiations which bring about structures entirely different from those known in normal tissues. We will call tissue formations of the first kind kataplasmatic galls or kataplasmas, and galls of the second kind prosoplasmatic galls or prosoplasmas, We will base the division of our abundant material upon the given differences between the former and the latter. Even with the help of this principle of division we will not be able to set up two entirely distinct groups, but with its use we will only rarely be uncertain as to whether the separate gall forms belong to this or that group. One could perhaps add to those galls, conceived as transitional between kataplasmas and prosoplasmas, the others, which, in spiteof their very simple tissue structure, develop "new" characteristics - in that the cells show abundant anthocyanin content, instead of being colorless or containing chlorophyll, or cells occur in them abnormally rich in cytoplasm, starch content etc. We will observe here that "typical" and unquestionable prosoplasmas often contain other cell-forms than those of the corresponding tissue of normal plants and that further the different kinds of elements participating in their construction are united into well-defined zones.

It is to the interest of a natural classification to consider the morphological characteristics of galls together with their histology. We will show that galls with kataplasmatic tissue characteristics hage no definite outer forms and no definite size. Heteroplasmatic galls show varying sizes and forms just as do callus tissues, formations of wound-wood and the fields of Erineum galls. We find, however, where galls of prosoplasmatic tissue structures are involved, that the outer appearance of the galls assumes "new" characters, being characterized by definite proportions of size and form. Kataplasmas are often produced by the action of parasitic fungi, which in the inner part of the host plant take up a field of distribution of varying extent, or after infection by animals which live freely on the upper surface of the diseased organ and by their wandering can indefinitely enlarge the field of their stimulation. Prosoplasmas are produced by the action of domiciled organisms, the extent of the field of stimulation remaining the same under all circumstances. Further, the different effective periods of the stimuli,which produce the galls, must be considered. The stimulus caused by producers of prosoplasmas is felt only in definite phases of their development, which, in various species, is enacted in a certain number of
(192) weeks and months, while any constant period of stimulatory action seems absent in kataplasmas the producers of which can often grow to be many years old and still be effective. We will be able to explain the histological differences between kataplasmas and prosoplasmas only by the specific quality of the effective gall-stimuli. But we will venture to trace the constancy, or rather the variability of the form and size proportions in different gall-products to the temporal and local extent of the effect of the stimulus.

Finally, a few words more concerning the etiology of galls. Naturally, nothing at all concerning the factors actually effective is indicated by the statement that these galls are produced after the infection of vegetable tissue by any parasites. Usually injury to the plant organs goes hand in hand with infection. Indeed many galls very strikingly resemble tissues produced after injury. This phenomenon becomes clearly evident in those cases, for instance, in which are involved diseased products of the cambium, influenced by parasites. In very many other galls, the structure of which exceeds the kataplastic character of wound tissue, at least the first stages of development resemble callus tissue. The fact that, in the production of prosoplasmatic galls, new processes of differentiation and formation must be added to those known for callus, proves satisfactorily, however, that still other stimuli besides traumatic ones must often participate in the formation of galls. Besides this, there are many galls in which it can be demonstrated that infection takes place without injury to the vegetable tissue, in which therefore all traumatic influences are excluded even from the beginning. The gall stimuli are undoubtedly of a chemical nature; some unknown substances, excreted by the parasite, incite the cells of the host plant to growth and cell-division and under certain conditions the products of division to different processes of differentiation. We know as yet nothing definite concerning the chemical character of the substances acting here. Up to the present, all attempts to cause gall formation by artificial inoculation with substances of known composition have failed. Unfortunately experiments, made with the contents of the "poison sac" of the leaf wasp in the endeavor to call forth "artificial" gall formations, have as yet given no positive results[1].

Disregarding the fact that the wound stimuli, preceding the formation of various galls, enclose within themselves a complex of many factors the significance of which is still but little known, an analysis of the factors active in the formation of galls was not perfected even with the discovery of traumatic stimuli and of the action of gall poisons. It is to be hoped that future experiments will throw light on the question as to whether the tissues of the plant in their normal condition are always susceptible to chemical stimuli or whether, in the formation of galls, they are often made susceptible to stimuli of other kinds only by traumatic interference and its results. It will be necessary to test further the questions as to whether the stimuli or contact proceeding from the larvae, which wan-
(193) der about inside the half-grown gall, are not also important in the further development of the gall, or whether it is possible, and in which cases it is possible, for the larvae to bring wound stimuli into effect by grazing upon the innermost tissues, thereby causing a new production of tissue;- whether the excrement balls, thrown off by the inhabitants of the galls, can act as a fertilizer, whether new stimuli proceed from these, etc.

We know but little, at any rate, about the capacity for reaction against gall poisons possessed by definite plants and definite tissue forms, because, in judging of this, we are still dependent upon the investigation of the new formation of tissue produced in nature and because the gall-insects cause their virus to act only on a definite substratum. On this account the question, as to whether tissues other than the ones

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[1] Beyerinck, Ueb. d. Cecidium v. Nematus Capreae auf Salix amygdalina Botan. Ztg., 1888, Bd. XLVI, p. 1.

preferred by them are also capable of reacting in the same way, must remain unanswered. We will be fully informed as to many of the questions referred to here only when it is possible to produce galls artificially on various plants and parts of plants under varying external conditions. Then we will be able to test experimentally all parts of plants as to their capacity for the formation of galls as we are now able to do in the formation of callus.

Looking back at the speculations of the nature-philosophers (Redi), we find that the assumption of an expecial poisonous action has always played the chief role in the attempt at explaining the genesis of the galls. Malpighi[1] assumed that the insect producing the gall excretes a poison which causes a fermentation of the content of the infected plant; this fermentation exciting the abnormal growth which leads to the formation of galls. Reaumur[2], to whom the secretion furnished by the gall insects seemed too scanty to cause such extensive new formations, thought that a kind of suction was produced by the gall-producers and inhabitants, which caused the juices of the plants to flow toward the place infected. According to him, a rise in temperature takes place at the place of stimulation, which favors tissue growth, and the theory stated by Malpighi has been proved capable of further development; Lacaza-Duthiera[3] returned in every detail to Malpighi's theory and explained galls as the products of the action of different kinds of poisons. Darwin and Hofmeister[4] later expressed the same opinion about the formation of galls. If the traumatic stimuli, which undoubtedly participate in the formations of many galls, were overlooked or given too little importance by the authors named it may be explained directly by the fact that their attention was directed first of all to the complicatedly constructed prosoplasmas. We will be obliged to return often to the similarity of many simply constructed galls (kataplasmas) to wound tissue; which favors the theory that traumatic stimuli participate in the formation of galls.

(194) All previous attempts to produce "artificial" galls by inoculation with different poisonous substances have failed. Compare, besides Bacerinck (see above), reports by Kny, Kustenmacher, Laboulbena, etc.[5]

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[1] Anatome Plantarum, London 1675-79.

[2] Réaumur. Mém. p. servir. à l'hist. d. insects. T. III, mem. IX u. X.

[3] Lacaza-Duthiers, Rech. pour servir a l'histoire des galles. Ann. Sc. Nat. Bot., 1853, 3me ser., T. XIX. p. 273.

[4] Darwin, On the origin of species. 5th edit., 1869, p. 572. Hofmeister, Allgem. Morph. d. Gew., 1868, p. 634.

[5] Kny, Ueb. künstl. Verdoppelung des Leitbündekreises im Stamm. d. Dikotyl. Sitzungsber. Ges. naturf. Fr., Berlin, 1877, p. 189. Küstenmacher, Beitr. z. Kenntn. d. Gallenbildungen etc. Pringsheim's Jahrb. f. wiss. Bot., 1895, Bd. XXVI, p. 82. Laboulbene, Essai d'ume theorie sur la production d. div. galles veget. C. R. Acad. Sc. Paris, 1892, T. CXIV, p. 720.

The parasites, under whose influence abnormal tissues are produced, are drawn from the plant and animal kingdoms. ("Phyto-cecidia" - "Zoccecidia"). The higher plants take part here by means of the Loranthaceae, while among the lower plants fungi especially come into consideration as incitors of gall formation. The animals which produce galls belong among the worms and the Arthropoda - the greatest majority by far among the latter. Mites and insects especially produce the most diverse galls on the most widely different kinds of plants. The Diptera and Hymenoptera play the most prominent role and among the latter belong the gall wasps (Cynipida) which can produce the most complicated of all gall formations. Further the Hemiptera should be named, among which are found many gall-producing leaf lice and shield lice, and finally the butterflies and beetles, of which, however, only a small number of representatives are known to produce galls.

In our histological observations, we can enter only very briefly into the nature of the producers of galls. At times it will be demonstrated that parasites, closely inter-related can produce the most different kinds of heteroplastic tissues. At any rate, fungi galls belong almost entirely among the kataplasmas[1], on the other hand, the galls of the Cynipida belong predominantly among prosoplasmas, while galls of both kinds are produced in large numbers by Diptera and Xymenoptera. Also, among prosoplasmas themselves, fixed relations between the quality of the abnormal tissues and the systematic position of the producers of the gall are neither very numerous nor striking; thus, for example, the leaf-wasps which produce galls of a simple structure are most closely related to the Cynipida, whose complicated products will fully occupy our attentions.

Plants capable of producing galls, are found represented in all groups of the plant kingdom, sometimes more abundantly, sometimes less so. Cryptogams, in comparison to phanerogams, must be distinguished as being especially poor in galls and the few which they develop have a simple histology. Among phanerogams, the dicotyledons form the group which has galls most abundantly, the representatives of which are capable of developing kataplasmas and prosoplasmas in equal quantities. The galls on trees and shrubs are universally more varied in form than are those of bushes and herbaceous plants. Quercus and Eucalyptus apparently belong to the plant genera which have most abundant galls.

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[1] Compare for exceptions or disputed cases p. 211.

a. Kataplasmas.

We will term kataplasmas those galls of any origin whatever, which are distinguished from the normal tissue of the corresponding organs by the small amount of their tissue differentiation. The differentiation of the single cells corresponds to that mentioned above in callus and wound-wood tissues. The tissue of kataplasmas consists often of abnormally large cell elements, the union of which usually gives a thin-walled, often entirely homogeneous parenchyma, or approximates it. Further, kataplasmas are characterized by their lack of any definite characteristic form or regularly recurring size.

Among kataplasmas belong first of all almost all Phytocecidia; since, among the plants which produce galls, only a very few are known as yet through the action of which prosoplasmatic structures may arise.

> We should mention as the most important gall producer among Myxomycetes, the producer of the club root of cabbage,- Plasmodiphora Brassicae. Ball-like swellings of various forms and sizes are produced on the roots of Brassica and other Cruciferae. According to Gobel, Tetramyxa parasitica, produces tuberlike swellings on Ruppea, Sorosphaera Veronicae Schröter moderately strong outgrowths on the roots and peticlos of different Veronica species. According to the recent investigations by Toumay, the goitres of many fruit trees etc. are the products of a slime-fungus - (Dendrophagus globosus).[1]

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1. The most important literature on myxomycete galls,- Woronin, Plasmodiophora Brassicae, Pringsheim's Jahrb. f. wiss. Bot., 1878, Bd. XI, p. 548. Nawaschin, Beob. üb. d. fein. Bau u. Umwandlg. v. Plasmodiophora Brassicae u. s. f. Flora, 1899, Bd. LXXXVI, p. 406. Göbel Tetramyxa parasitica, Flora, 1884, Bd. LXVII, p. 517. Schröter, Phytomyxinae. Engler-Prantl's Natürl. Pflanzenfam. I, 1, p. 5. Toumay, An inquiry into the cause and nature of crown-gall. Arizona Exper. Station, 1900, Bull, XXXIII. Müller-Thurgau. II, Jahresber. Versuchsstat. Wadensweil.-- The disease of agave leaves (Tylogonus Agavae, Athens 1888) described by Miliarakis might well not be traceable to parasites. In investigating microscopically the brownish cushions, occurring extraordinarily numerously on the leaves, I found no traces of a slime fungus (Professor Miliarakis most kindly sent me the material). Rather I believe that the swellings, just like the well known black buttons on the leaves of Gasteria and other succulents, are related to "hyperhydric" tissues (see above p. 83). Among the abnormally enlarged cells there results a very abundant formation of wound cork, by which the diseased parts of the leaf tissue are separated from the healthy ones. Further investigation would be desirable.- The agave disease studied by Miliarakis not only occurs in Mediterranean countries but also in German botanical gardens etc.

Certain bacteria are known to incite the roots of the Leguminoseae to the production of extensive tubercles, consisting of parenchymatic, undifferentiated tissue. We will not stop[1] to consider the question, whether this is to be included among the new pathological formations, or not. We will speak later of the swellings caused by bacteria on Pinus halepensis and Olea europaea.

(496) Of the Eumycetes, all the chief groups come under consideration here; numerous Phycomycetes, Uredineae, Ustilagineae, Ascomycetes and Basidiomycetes develop kataplastic plant galls. The galls of the Synchytriae (Phycomycetes) were mentioned above (p. 108). Among the Uredineae, I refer, for example to the Aecidia galls of Viola, Berberis, Rhamnus, Urtica, to the branches of Vaccinium Vitis Idaea attackek by Calyptospora Göppertiana, to those of Juniperus infected by Gymnosporangium, to the products of Peridermium Pini, which resemble wound-wood, etc, and to the bizarre branching, produced by Caeoma deformans on Thujopsis. Of the galls of the Ustilagineae, I will name only the smut boils on maize inflorescences, (Ustilago Maydis) the galls of Ustilago Treubii[2], those of various Urocystis species above and below ground. Of the Ascomycetes, especially the primitive forms (protomyces, Exoascus) come under consideration as producers of galls. Besides these, still a few representatives of the Carpoasci which produce canker-like woody excrescenses (canker of the larch produced by Dasyscypha Willkomii etc.) Of the Basidiomycetes, various Exobasidium species are of interest to us as producers of galls.[3]

Tissue excrescences caused by Algae are known especially for Cystoseira opuntioides and C. ericoides, upon which according to Valiante[4] and Sauvageu[5] Streblonemopsis irritans and Ectocarpus Valiantei live par-

Of the higher plants the Loranthaceae are almost the only ones coming under consideration here. They often produce enormous gall formations, the so-called wood roses, on their host plants. The infected branch of the

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1. Compare Frank, Lehrbuch der Botanik, 1892, Bd. I, p. 268 ff; Therein also many further literature references. For variously formed "tubercles" compare the dissertations by O. Schwan, Ueber d. Vorkommen v. Wurzelbakterien in abnorm verdickten Wurzeln v. Phaseolus multiflorus. Erlangen, 1898. - On the tubercle outgrowths inhabited by bacteria, found on many marine algae, compare above p. 154, note 2.

2. Solms-Laubach. Ustilago Treubii. Ann. Jard. Bot. de Buitenzorg, 1887, T. VII, p. 79. We will speak again of this gall in the section on prosoplasmas.

3. Compare especially the text book by v. Tubeuf, Pflanzenkrankh., durch kryptogame Parasiten verursacht, 1895, Further literature will be named later.

4. Valiante. Sopra un Ectocarpea parasita della Cystoseira opunticides - Streblonemopsis irritans. Mittle. Zool, Stat. Neapel, 1883, Bd. VI, p. 489. Compare the illustrations in Engler-Prantl, Naturl. Pflanzenfam. Bd, I, 2, p. 189.
5. Sauvageau. Sur quelqu, algues phéosporées parasites. J. de Bot., 1892, T. VI, p. 57.

host grows out in a ridge around the clasp shield of the parasite (Phoradendron etc.), thereby producing radiated cup-like excrescences, corresponding to the form of the parasite.[1]

The Zoocecidia, which may be classed among kataplasmas are produced especially by worms (Nematodes) and also by mites and insects.

Nematode galls, produced by Heterodera and Tylenchus, are found on the aerial and underground parts of the very many different plants. H. radicicola is important because of its distribution; it produces knob-like galls on the roots of monocotyledons and dicotyledons. Nematode galls (produced by Tylenchus fucicola) are said to occur also on Ascophyllum nodosum[2].

Of the mite galls, I consider as belonging here the fleshy (hyperplastic) curlings of the leaf edges of Tilia, Crataegus, Pirus and many others, the bud swellings of Corylus avellana, the galls on the tips of shoots, which are composed of swollen leaves and the so-called pustule galls abundant on Pirus communis on Sorbus and many others, many "Erineum" galls, consisting of multicellular cones and ridges, such as the so-called Erineum populinum, and still others.

The Diptera often produce complicated galls with a prosoplasmatic structure; the kataplasmas called forth by them repeatedly have the form of fleshy curlings of the leaf edges (for example, on Polygonum, Populus tremula and others) and swollen tips of shoots (for example, on Glechoma) or there are produced by a uniform swelling of numerous leaf bases or inflorescence stalks, clustered forms, resembling pineapples, termed pinapple-galls. Cecidia of this kind have been found on various Cruciferae (for example, Nasturtium, Barbarea) and others.

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1. Compare the illustrations in Engler, Loranthaceae, Naturl. Pfl.-Fam., Bd. III, I, p. 61.

2. Statements concerning nematode galls are to be found especially in Frank, Die Krankh. d. Pfl., 2. Aufl., 1896, Bd. III, p. 12. C. Müller, Mitteil. üb. d. uns. Kulturpfl. schädlichen, das Geschlecht Heterodera bildenden Würmer. Landwirtsch. Jahrb., 1884, Bd. XIII, p. 1. Ritzama Bos, Die Aelchenkrankheit d. Zwiebein (Allium Cepa). Landw. Versuchsstat., 1888, Bd. XXXV, p. 35. Atkinson, Nematode Root-galls, J. Elisha Mitchell. Scient. Soc., 1889, Vol. VI.-- Many new statements in Sorauer's Zeitschr. f. Pflanzenkrankh.- For Tylenchus fucicola compare Murray, Phycological Memoirs, 1892, Part I, p. 21.

The Hemiptera must be mentioned because of the gall-producing Aphids (leaf-lice) and Psyllodes (leaf-fleas). Here too we find thickened, curled or swollen leaves (for example, on Crataegus, Fraxinus) knot-like swellings on roots (Phylloxera vastatrix on the roots of the grape) and canker-like woody-excrescences, for example on Pirus malus and Fagus silvatica after colonization by Schizoneura lanigera (the blood-louse) and Lachnus exsiccator (the beech-tree louse). The shield lice, in so far as they cause the formation of galls, produce kataplasmas in the form of canker-like excrescences and the like (on oaks and beeches, Coccus Cambii and C. Fagi) but are of little significance. Further, the role played by bugs (Rhynchota), as well as Coleoptera and Lepidoptera as gall insects is subordinate. The Hymenoptera (leaf wasps and gall wasps) almost exclusively produce gllas of a prosoplasmatic character and will be discussed later. Finally I will mention the gall of a Copenod (Crustaceae) on Rhodymenia palmata[1]

We find plants in all groups of the plant kingdom , capable of producing kataplastic galls. It is noteworthy that the lower plants bear galls exclusively of a kataplasmatic character, while on higher ones, kataplasmatic and prosoplasmatic structure abound. The above-named galls on marine algae are of very simple structure and indistinguishable histologically from the
(198) excrescences produced after injury. (See above p. 154). The same is apparently true of the galls of fungi, if I may include here the abnormal tissues of Agaricus campestris[2] produced by the excitor of the "Molle". The galls of woods and ferns, so far as known, are predominantly (or entirely?) of a kataplasmatic nature.[3]

Kataplasmatic galls are found on all parts of plants: roots and sprouts, stalks, leaves, inflorescences and fruits are deformed by them. Proportions of size and form, as above said, vary within wide limits in galls of the same kind; sometimes whole leaves are transformed; whole inflorescences and large

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1. Barton, J. of Bot. 1891.

2. On diseased mushrooms, Mycogone rosea and Verticillium are found as parasites. See also Costantin and Dufour: La Molle, maladie de ch. de couche. C. R. Acad. Sc. Paris 1892, T. CXIV, p. 498. Costantin: Sur quelques maladies du blanc de Ch. Ibid. p. 849, There also further literature references.- For galls on fungi compare also Vogler, Insekten auf Polyporus, Illustr. Zeitschr. f. Entom. 1899, Bd. IV, p. 345, and others.

3. For the forms of galls occurring in different Pteridophytes, Darboux and Houard. Catal. systèm de Zoocècidies (Paris 1901) should be compared. It must remain open to doubt whether the many chambered gall of Pteridium aquilinum (not well known to me) produced by a Cynipide, also belongs among kataplasmas. The "pseudo-bulbils (Strasburger's, Einige Bemerk. üb. Lycopodiaceen, Botan. Zeitg., 1873, Bd. XXXI, p. 105) produced on Selaginella pentagona by a diptera, are apparently kataplasmas. For their morphological character, compare Strasburger's work already cited.

sections of shoots are brought to hyperplastic development; sometimes more or less extensive parts of single organs. Ball-like swellings are often produced, or isolated galls, often clustered complexes. Since the area of infection in the case of different gall producers has no constant size, tiny pustules are often produced or often extensive deformations, corresponding to the amount to which the parasites are distributed on or in their host plants.

The histology of kataplasmas needs no detailed description. Almost universally, aside from a slight tissue differentiation, the compostion of kataplasmas is made up of abnormally large cells.[1] As in all gall-formations the cells of the kataplasmas also show an abundant albumen content. They often contain red cell-sap pigment. Especially striking is the accumulation of starch which we find again in very different kinds of galls,- in the rupture of the cabbage as in the tubercles of Leguminoseae roots, in aphid galls etc. Since the anatomical structure of kataplasmas shows essentially everywhere the same structure forms, in their slight differentiation, it suffices to explain the essential points by a few examples.

1. Primary Tissues.

The difference between normal and infected tissues is very obvious, when leaves and parts of stalks are involved, which if undisturbed, would develop diversely differentiated tissues in well-separated layers.

In leaves etc. infected by fungi (Mycocecidia) the otherwise very evident difference between epidermal and ground tis-
(199) sue cells is often only weakly defined. In the mesophyll itself the difference in formation between palisade parenchyma and spongy parenchyma is often entirely lost. In other cases a slight differenece in the cells of the upper and lower mesophyll layers is retained. It is often the case that the cells of the spongy parenchyma are prevalently incited by infection to a rich proliferation. The illustration by Woronin, reproduced here, shows very clearly the difference between normal and diseased mesophyll: the parts of the leaf of Vaccinium Vitis Idaea infected by Exobasidium Vaccinii are greatly distended(fig. 74a) developing a tissue composed of very large cells, poor in chlorophyll or free from it (fig. 74b); the uppermost cell layer of this corresponds to a hypertrophied palisade layer. The tissue continuity of the cells is the same in all parts of the leaf, a difference between thick and porus spongy tissue (fig. 74b- at the left) being scarcely recognizable in the part of the leaf infected. In some cells of the gall a red coloring matter is developed. That
(200) even the mesophyll of the conifer needles may be brought to excrescence by fungi has been proved by Wörnle, in the leaves

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1. It was mentioned above(p. 117) that in cases of weak infection, or unfavorable developmental conditions, the cell divisions are absent, and instead of hyperplastic excrescences only hypertrophic changes can occur.

of *Juniperus communis* attacked by *Gymnosporangium juniperinum* (the form living in the needles).[1]

The same arrestment of tissue differentiation is found in Zoocecidiae. Figure 75 shows a cross-section of a leaf of *Crataegus oxyacantha* after colonization by *Aphis oxyacanthae*, a leaf-louse. On the infected swollen planes, usually strikingly reddened, the mesophyll is increased several cell layers, any distinct formation in the upper and lower layers is entirely lacking, and the epidermal cells are approximately as large as those of the mesophyll. Its cell walls are often pretty thick and apparently very rich in water.

In all cases the hyperplastic cell increase is limited to the mesophyll while the epidermis participates only in so far as its cells are often considerably enlarged, cross-divisions taking place only exceptionally. That the ground tissue tends to a greater proliferation than does the epidermis has been repeatedly confirmed above and will be reaffirmed later.

While, in most cases, in the proliferation of the mesophyll as in pure hypertrophic changes (see above), the chlorophyll content degenerates completely or in great part, there
(201) are [2] a few exceptions among galls in which the chloroplasts are retained. Such exceptions are shown by the so-called pustules of Pirus, Sorbus and others. Through the action of gall-mites mesophyll is forced out into elliptical swellings, the single cells are greatly elongated and many times divided, their content retaining its normal green color. In the places infected the leaf tissue consists of porous green, confervoid rows of cells. The excrescences of the assimilatory tissue in

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1. Wörnle. Anat. Unters. der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forstl.-Naturwiss. Zeitschr., 1894, Bd. III, p. 68. Of the other literature, compare especially, Woronin, *Exobasidium Vaccinii*. Verh. naturforsch. Ges. Freiburg i. Br. 1867, Bd. IV, p. 397. Wakker, Unters. üb. d. Einfl. parasitcher Pilze auf ihre Nährpfl. Versuch einer pathol. Anat. d. Pfl., Pringsheim's Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 499. Further *Fentzling*, Morph. u. anat. Untersuch. der Veränderungen, welche bei einigen Pfl. durch Rostpilze hervorgerufen werden. Diss. Freiburg i. Br. 1892, Peglion, Studi anatom di alcune ipertrofe indotte dal *Cystopus canidus* in alcuni organi die *Raphanus Raphanistrum*. Riv. Pat. veg. 1892, Vol. I, p. 265. Smith, W. G., Unters.d. Morph. u. Anat. der durch Exoasceen verursachten Spross- u. Blattdeformationen. Gorstl.- Naturw. Zeitschr., 1894, Bd. III, p. 420. Therein a number of graphic illustrations, Molliard, Cécidies florales. Ann. Sc. Nat. Bot., 1895, 8me ser., T. I, p. 67. Strohmeyer, O., Anatom. Untersuch. der durch Ustilagineen hervorgeruf. Missbildungen. Dissertation Erlangen, 1896, Géneau De Lamarliere, S. l. mycocecidies du Roestelia. Rev. gen. de Bot., 1898, T. X. p. 225.

2. In contrast to the many cases already described of chlorophyll degeneration and its non-development, the present cases are of especial interest since there is no lack of food substances here for the colorless cells, or those poor in pigment. The cytoplasm is rich in protein and the cells are usually abundantly provided with starch meal. The causes determining the utilization of the food substances for the formation of chlorophyll are unknown.

the form of green emergences on the leaves of Crataegus oxyacantha (after colonization by Cecidonyia Crataegi) may also be included here.

The vascular and mechanical tissues undergo the same reduction in kataplasmas as does the assimilatory tissue. The vascular bundles in the parts infected are often only of very moderate extent; the single ducts often retaining the narrow lumina. The mechanical tissues, which under normal conditions protect the vascular bundles, are not developed (compare fig. 74). According to Wakker (loc. cit.) the collenchyma is lost in the infected stalks of Vaccinium Vitis Idaea (Exobasidium) in the stalks of Rhamnus frangula (Aecidium Rhamni) and Crataegus oxyacantha (Roestelia lacerata). In the same cases, the sclerenchyma also is lacking.

Finally, the hyperplastic excrescences of the pith should be mentioned. One especially conspicuous form is found in those produced by Aecidium Englerianum on clematis branches; parenohym atous cone-like protuberances are developed from the pith which break through the ring of vascular bundles and the bark.[1]

While in prosoplasmas all the cell divisions or at least the first ones, accompanying the formation of the gall, often show a definite orientation and produce regular cell rows, in kataplasmatic excrescences of the primary tissues regularly oriented cell rows are almost entirely lacking.

In very different kinds of galls, as in wound tissue (see above p. 166) bead-like structures occur on the outer surface of the cell-membrane, but nothing positive has been discovered as yet concerning their chemical composition.[2]

2. Secondary Tissues.

Of the secondary tissues, only the products of the cambium come under our consideration. In the formation of galls, either the living derivatives of the annual ring already formed are incided to division, or its own cells are used in the production of the kataplasmatic tissue; as described above in the formation of wound-wood. After infection with different fungi or after colonization by gall-animals, swellings are produced in wood and bark usually knob-like in form, or clustered (compare fig. 76), which resemble the canker formations
(202) produced after injury or frost, ("gall-wood"), or even brush-like excrescences of the branches develop,known as "witches-

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1. Lindau, Bemerk. üb. Bau u. Entwickelung von Aecidium Englerianum. P. Henn and Lindau. Engler's Jahrb., 1893, Bd.XVII, p. 43.

2. Compare also Noack, Ueb. Schleimranken in d. Wurzelintercell. einiger Orchideen. Ber. d. D. Bot. Ges., 1892, Bd. X, p. 645. Nypels. Notes de Pathologie végètale. C. R. Soc. Bot. Belgique, 1897, T. XXXVII, p. 246. ("prolongements de la membrane cellulaire").

brooms".

Abnormal Wood.

(203) The numerous woody-galls produced by many fungi (Gymnosporangium, Peridermium, Dasyscypha, Nectria, Agalaospora, etc.), parasitic phanerogams (Loranthaceae) and insects (Schizoneura, Lachnus, etc.) have been subjected in part to closer anatomical investigation. So far as known, all woody-galls are characterized by the abnormally abundant parenchyma development, recognizable in the structure of wound-wood.

Increase of the parenchymatic elements can be produced here and there by segmentation of the young derivatives of the cambium, which thus furnish groups of parenchymatic cells, instead of growing out into prosenchymatic xylem elements,- or by the corss-division of the cells of the cambium itself and the production, after further division, of parenchymatic products. Either the cambial cells are only changed in places as described, so that the cambial rays are broadened and their number seems increased,- or the cells divide over the entire area of infection, so that extensive, continuous masses of parenchymatic wood are produced. No difference in principle may be proved between Myoocecidiae (fungus-galls) and Zoocecidiae (animal-galls).

We will begin with an example from the list of Mycocecidiae.

As is well known, the gymnosporangia produce spindle-like or ball-like woody-galls on different species of Juniper (J. communis, Sabina, etc.) Wornle[1] has studied their structure thoroughly. According to his statements, the difference between spring and autumn wood is not expressed normally in diseased wood, the annual boundaries are scarcely recognizable. Besides this, the parenchymatic elements in the wood require themselves a noticeably broad space. Instead of being only 2 to 10 cells deep, the cambial rays in the parts of branches infected by Gymnosporangium clavariaeforme are often 10 to 20, even 60 cell layers depp, and as many as 3 cells broad. Still broader cambial rays are found in the tangential longitudinal section through the woody-gall of G. juniperinum shown in figure 77. Further variations from a normal condition are found in the hypertrophied parenchyma cells, which assume a "shapeless form" and disturb the radial arrangement of the tracheids (Wörnle, loc. cit. p. 146) and further in the occurrence of distended parenchyma-cell centers which Wörnle in one case found broadened to one sixth of the
(204) whole size of the branch. They extend partly in the direction of the cambial rays, partly in the vertical direction of the parenchyma of the cord. In cross-section it is clear that they are separated only by slender, tracheid-groups, often consisting of one row of cells. Wörnle's discoveries do not throw sufficient light on the development of these abnormal tissues. Yet I would like to assume that the first named, abnormally broad cambial rays are brought about by segmentation of the cambial cells, the last named parenchyma centers by

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1. Anat. Untersuch. d. durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forstl.-Naturwiss. Zeitschr., 1894, Bd. II, p. 68.

a uniform division of the young cambial daughter cells. In my opinion, the occurrence of isolated tracheid-groups favors this supposition. The parenchyma centres (G. juniperinum) are often followed, toward the periphery, by abnormally short and broad tracheids, furnished on all sides with numerous bordered pits.

Naturally, a division of the parenchymatic elements and the over-production of a woody-parenchyma can also occur without abnormal widening of the annual ring. Woody plants with fungous diseases furnish numerous examples of this. I wish to mention at this point the production of abnormal resin-canals which are known to be surrounded always by parenchyma tissue alone. Either the number of resin-canals is increased beyond the normal or they occur in wood which normally remains free from them. (cf. the abovesaid concerning wound-wood, page 176). Hartig[1] produced an increase of the resin-ducts in the diseased places of conifers, infected by Agaricus melleus. Anderson[2] produced the interesting proof, that the resin canals are increased not only in the places filled with the fungus mycelium, but in the whole plant, outside the infected areas. (Picea, Pinus, Larix).

In Abies pectinata, the wood of which is known to develop no resin-canals under normal conditions, such canals are developed after infection by Phoma abietina even above the constricted place of infection in the xylem;[3] this also occurs in Abies pectinata and Picea excelsa after colonization by Pestalozzia Hartigii. The abovesaid (p. 176) is supposedly true also of the structure of these abnormal resin-canals.

The transformation of wood into parenchyma is performed even more energetically by some Zoocecidiae.

Instead of a formation of parenchyma rays and parenchyma centres, we can prove a production of parenchyma to the greatest extent, in the case of many Hemiptera galls. Just as in the case of callus and wound-wood formation, all the cells, or, in the latter, the youngest daughter cells in extensive areas of the cambial mantel divide and furnish a tissue composed of isodiametric elements. While in the case of injury corresponding to an abrupt interference in the normally continued development of the tissues, the parenchymatic wound
(205) tissue directly joins the normal xylem, we find in the case of many galls, that the weak but continuously effective stimuli given out by the parasites make possible a gradual transition from the normal xylem to a homogeneous gall parenchyma.

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1. Krankh. d. Waldbäume, p. 13.

2. Ueb. abnorm. Bildung von Harzebehältern u. andere zugleich auftretende anatom. Verand. im Holz erkrankter Koniferen. Forstl.- Naturwiss. Zeitschr., 1896, Bd. V, p. 439.

3. Compare Mer, Rech. s. la maladie des branches du sapin, causée par le Phoma abietina. J. de Bot., 1893, T. VII, p. 364, also Anderson, loc. cit.

The structural conditions to be studied in the galls of the blood louse of the apple are very instructive. (Fig. 76) First of all, the mechanical elements are absent in the abnormal wood; instead of ducts and woody-fibres, numerous parenchyma cells are produced by division of the prosenchymatic elements, which in longitudinal sections show their developmental relation to the regular longitudinal rows. (Fig. 78a). As shown in the illustration, the single cells have pretty thick walls which are pitted. In the layers of gall-wood produced later, the single parenchyma cells are noticeably larger while a regular arrangement is no longer recognizable, and their walls remain delicate. (Compare fig. 78b). Instead of normal ducts, only isolated parenchymatic tracheids or others united into groups are formed, distinguishable from the delicately walled parenchyma cells by their size. Their membrane is pitted like that of a trachea, but often unlignified; the tissue structure reminds one of callus. (Fig. 67). In its entirety, the thin-walled woody parenchyma furnishes a soft swelling, wich in water, which can increase to such an extent that the bark is ruptured and the gall tissue laid bare[1]. The fact that the delicately walled woody parenchyma cells are multi-nuclear, as discovered by Prillieux (loc. cit.) is noteworthy.

The conditions in galls of the beech-louse, (Lachnus exsiccator) are similar to those of the blood-louse. R. Hartig[2] studied them closely. Here also is found tha same gradual transition from normal wood to homogeneous, parenchymatic gall-tissue.

Abnormal Bark.

While in many cases (galls of Schizoneura lanigera, etc.) the bark remains practically unchanged, in other gall-formations extensive bark excresences are produced, whereby the changes in tissue, essentially the same as in the formation of woody galls, consist of an abnormal production of parenchyma.

The Mycocecidia which should be named here, are produced by Eumycetes and bacteria.

It is seen in the galls of many Gymnosporangium-varieties that the bark and the wood form excrescences simultaneously. According to Wornle (loc. cit), in weakly grown branches of Juniperus communis, Gymnosproangium clavariaeforme incited the bark rather than the wood to a tissue production. Hand in hand with the superabundant formation of parenchyma, proceeds an arrestment in the formation of the parenchymatic, mechanical fibres. They remain thin-walled and decrease in number. Therefore in a comparison of normal with abnormal barks, essentially the same points of consid-

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1. Prillieux, etude des altèrations prod. d. le bois du pommier par les piqures du Puceron langière. Ann. Inst. Nat. Agronom., 1877, T. II, p. 39.

2. Die Buchenbaumlaus (Lachnus exsiccator Alt.) Untersuch. aus d. forstbot. Inst. München, 1880, Bd. I, p. 151.

eration exist as in that of normal with abnormal wood.

An especial class of tissue excrescences of a kataplastic nature, usually produced from the bark tissue of the branches, more rarely in other places, is formed by the parenchymatous, wood-like excrescences, occurring on the olive. (Olea europaea) and on the Aleppo pine (Pinus halepensis) and, according to the unanimous statements of French and Italian authors, caused by bacteria.[1] Provided that the present statements concerning the etiology of the swellings hold true,[2] an especial significance accrues to these "tumeurs a bacilles" in so far that, according to our present knowledge, the action of pathogenic bacteria on plants consists chiefly in dis-organization and necrosis and is not connected with formative stimulatory
(207) effects. Besides the bacteria tubercles here named only those of the Leguminosae and the leaf swellings on tropical Rubiaceae observed by Zimmerman[3] come into question as exceptions to the rule.

The bacteria galls of the olive are mostly produced on branches 1 to 15 years old, more rarely on roots, leaves or fruit and indeed in such a way that, in the case of branch infection, a colony of bacteria is first visible near the cambium or in the bark tissue, by which the adjacent cells are incited to division. The proliferating tissue cases the rupture of the superficial cell layers and grows out gradually to a knot, as large as 2cm. in diameter. The swellings consist primarily of predominantly thin-walled parenchyma, in which are scattered thick-walled cells with woody and pitted membranes. This becomes woody later and groups of irregularly arranged, short-membered ducts are formed, reminding one of the histology of wound-wood.

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1. Literature:- Arcangeli, Sopra la Malattia de ll' olivo detta volgarmente "Rogna". Pisa, 1886. Savastano, Les maladies de l' oliveir et la tuberculose en particulier. C. R. Acad. Sc. Paris, 1886, T. CIII, p. 1144. Savastano, Tuberculosi, Iperplasi e Tumori dell' olivo. Annuario d. R. Scuola sup. d'agricolt. Portici, 1887, Vol. V. Fasc. IV (Therein, also full literature references.) Prillieux Les tumeurs à bacillies des branches de l'olivier et du pin d'Alep. Rev. gen. Bot. 1889, T. I. p. 293. Vuillemin, Sur une bacteriocecidie ou tumeur bacillaire du pin d'Alep. C. R. Acad. Sc. Paris, 1888, T. CVII, p. 874. Sur les relations des bacilles du pin d'Alep avec les tissus vivants. Ibid. p. 1184.

2. Savastano (Les maladies de l'olivier, hyperplasies et tumeurs. C. R. Acad. Sc. Paris, 1886, T. CIII, p. 1278) describes very similar swellings on the olive which are produced without the participation of any parasitie whatever.

3. Ueb. Bakterienknoten in d Blättern einiger Rubiaceen. Pringsheim's Jahrb. f. wiss. Bot., 1901. Bd. XXXVII, p. 1. Brzczinski attempted recently to trace canker-like excrescences of the apple (Nectria) back to the activity of bacteria (Etiologie du chancre et de la gomme des arbres fruitiers. C. R. Acad. Sc. Paris, 1902, T. CXXXV, p. 106)

They show a tendency to the "gnarl formation" described above in detail.[1] In old age, a disintegration of these knots takes place, in such a way that a depression is formed in the middle of the swelling.

The bacteria swellings of the Aleppo pine, fast becoming a menace to wooded districts of the maritime Alps, are still larger than those of the olive and more regularly rounded. No disintegration of the central parts takes place later. According to Pfillieux the formation of the knots proceeds from the bark tissue; histologically they also resemble wound-wood.

As an example from the list of Zoocecidia, I will mention the gall of Chermes fagi, the beech wooly louse, which Hartig[2] has closely investigated. The gall-formation here begins directly beneath the cork and can advance even to the woody-body; all parenchymatic elements of the bark, including the tissue of the cambial rays grow out extraordinarily vigorously and divide actively in a tangential direction, so that long, multicellular, regularly radial rows are produced (compare fig. 79), by which the stone cells and the prosenchymatic elements of the bark are pushed from the normal position. He found in the bark excresences of Gold-ribes (p. 80) that similar changes may also be produced by hypertrophy of the parenchymatic bark elements.- The case of the beech-Chermes gall again illustrates very distincly the great correspondence between kataplasmatic galls and callus tissues. The abnormal bark tissues illustrated in figure 79 show the greates similarity with the bark callus excrescences de-
(208) scribed above for Populus. In both cases a constancy of direction of cell-division and a lack of differentiation of tissues is common.

Bark excresences, the cells of which display no regular arrangement, are produced by different Ceutorrhynchus species, especially C sulcicollis, the "kohlgallerrüsselkäfer" (cabbage weevil) on the roots of various Crucifera (Brassica, Raphanus). The wood too is developed abnormally abundantly on the side infected.[3]

(209) Witches Brooms and Stag Head.

An especial class of galls is formed by the so-called witches-brooms (or Thunder-bushes), branch-

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1. Prillieux, loc. cit. p. 298--"des faisceaux sinueux de bois traumatique a cellules courtes, qui s' enroulent autour de centres de formation. Ils apparaissent ca et la dans la masse du parenchyme, au voisinage des points ou se montrent les colonies de bacilles. Ces enroulements de fibres ligneuses sont tout a fair comparables à ceux des madrures des bourrelets qui se produisent au bord des plais des arbres et au plancher ligneux qui s' organise dans la moelle, à la base de certaines boutoures." (Compare above p. 180)

2. Die Buchen-Wollaus (Chermes fagi Kltb). Untersuch aus d. fortsbot. Inst. München, 1880, Bd. I, p. 156.

3. Frank, loc. cit., p. 288.

excrescences of shrub or nestlike habit of growth, in which is involved an over-production of whole organs/ Questions of morphological interest are especially connected with these. (Compare Goebel, Organographie).

Among them we find Mycocecidia. Witches brooms are produced on Alnus, Betula and Prunus, as well as on various ferns after infection by Exoascaceae, on Abies species, on Acacia and Berberis by the action of various Aecidiae, or Thujopsis dolabrata by Caeoma deformans etc. Among the Zoocecidiae, for instance, the abnormal ramifications of the Syringa shrubs attacked by the mite-disease, bear a great similarity to the above mentioned fungus galls. Giesenhagen[1] has shown that the formation of witches-brooms does not always proceed from normal buds but can also be produced from leaves as adventive formations, (Taphrina on ferns). Studied macroscopically, many forms of the witches-brooms may be recognized as "arrested developments". Thus, according to Tubeuf, the witches broom of Caeoma deformans consists of leafless branches[2]. According to Giesenhagen, fleshy, wart-like or antler-like forms, always entirely leafless, which are traversed by a vascular-bundle cord, are produced by Taphrina Cornu cervi on the leaves of Aspidium aristatum[3]. Investigated microscopically, all witches-brooms show the characteristics of kataplasmatic galls. The different tissue forms, of which the abnormal branchlets and their leaves are composed, remain below the corresponding normal tissues in differentiation.

Some arrestment phenomena correspond to those already described (p. 32). The witches-brooms of the pitch pine caused by Aecidium elatinum bear needles, the hypodermis of which remains undeveloped and the mesophyll homogeneous. The development of bark fibres in the trunk is retarded, but that of the parenchymatic elements, on the contrary, is greatly favored. The pith is abnormally abundant, the bark perhaps twice as thick as in normal parts, also the number of resin-canals is abnormally large[4]. Resin-canals may occur even in wood, which in the spruce would have none normally, through the action of the witches-broom fungus[5]. The anatomical conditions of the Exoasceae-witches brooms[6] are of a similar nature. The parenchymatous tissues,- pith, hypodermis - are greatly increased, wood

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[1] Ueb. Hexenbesnn an tropischen Farnen, Flora, 1892, Bd. LXXVI, p. 130.

[2] In this they resemble the cylinder-gnarls of Ginkgo, described above p. 185.

[3] The antler-like malformations described by Miquel (Linnaea 1853, Bd. XXVI, p. 285) are, according to Solms-Laubach, deformed leaves of a Hemiptera gall (Ann. J. Bot. Buitenzorg, 1887, Vol. VI, P. 88).

[4] According to Hartmann, Fr. Anatom. Vergl. d. Hexenbesen d. Weisstanne mit den norm. Sprossen derselben. Dissertation Freiburg i. Br.,1892. Anderson, loc.cit.also DeBary, Ueb. d. Krebs u.d.Hexenbesen d. Weisstanna,Bot. Ztg.,1867,Bd.XXV,p. 257.

[5] Cf. Mer and Anderson loc. cit.

[6] Cf. Rathay, E., Ueb. d. Hexenbesen d. Kirschbäume, etc. Sitzungsber. Akad. Wissensch. Wien, 1881, Bd. LXXXIII, 1. Abt. p. 267 and especially Smith loc. cit.

and bark are traversed by abnormally broad cambial rays, the ducts have short members, the wood-fibres wide lumina, and are often cross-divided and thin-walled. The bast fibres are few or entirely lacking. Tubeuf found in the
(210) irregularly forked branches of the Caeoma witches-brooms on Thujopsis, a woody structure characterized by a parenchyma formation, similar to that found by Wornle in the galls of the Gymnosporangia.

According to Giesenhagen, the leaves of the fern-witches-Broom are distinguished from normal ones by a simpler tissue structure. For instance, the stomata are lacking in the abnormal leaves, produced by Taphrina Laurencia on Pteris quadriaurita. Tubeuf[1] also verified similar arrestment phenomena in the diseased buds of Syringa shrubs bearing witches brooms.

In many respects, the stag head of the willows, produced by leaf-lice (Aphis amenticola), are similar to witches-brooms. These have often been described since Malphigi and were recently thoroughly investigated by Appel[2]. In them, cauliflower-like, ball, or tuft-like accumulations of branches are involved, which can become 10 to 20 cm. and more long. The branchlets, of which these are composed, are always short and richly set with small, often somewhat thickened leaves. The axes are soft and rich in parenchyma, the leaves contain undifferentiated mesophyll, - therefore, the characteristics of kataplasmatic galls are repeated here. The stag heads originate either from normal buds, or, as Appel has shown single thickly massed new vegetative points, produced on the pistillate inflorescences in the interior of the ovary, as well as outside the carpel - leaves on the gland spots and on the stalklet of the ovary and grow out to the above described abnormal branch-excrescences. On account of the adventitious character of their origin, stag heads are comparable to the witches-brooms on fern-fronds, which Giesenhagen described.

b. Prosoplasmas

We will term prosoplasmas those galls which are characterized first by the fact that their tissues, in their differentiation, do not show the histology of arrestment-formentations nor of callus tissues, but form new kinds differing entirely from the normal,- and then also by the fact that definite proportions of form and size, characteristic for the species, are always repeated in them. Therefore, in this external form, prosoplasmas display something independent, well-defined, distinguished obviously from the organs of the normal plant-body; something "new" and independent, however, is shown also by their inner structure.

If we compare the histology of prosoplasmas with that of the above described kataplasmas and callus-formations (in the widest sense of the word) we can define prosoplasmas as those (hyperplastic) new formations of plants, in which occur also histological characteristics other than those known as yet in arrestment and callus formations. Hyperplastic tissues of this
(211) kind have been found up to the present only in the excrescences

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[1] Die von Milben erzeugten Hexenbesen der Syringen. Flugblatt.

[2] Ueb. Phyto- und Zoomorphosen. Dissertation Wurzburg (Königsberg), 1899.

produced by parasites. They are the most richly differentiated of all known abnormal tissue formations. Therefore we will take them up at the end of our consideration.

The galls to be treated of in the present section are almost exclusively Zoocecidia. Of the animals producing galls, only the arthropods come under consideration here, since the galls produced by worms (Nematodes) always have a kataplastic structure.

The study of the animals which produce galls brings us but little information of importance for consideration, since we are concerned only with the diseased products of plant organs. It will become clear that the systematic position of the gall animal in one or another group of the arthropods can determine no regular connection between the form and structure of the galls produced by them.

The mites, mentioned as producers of different kinds of kataplasmas must be considered also under prosoplasmas. Their products are very simple in form, as in structure.

The diptera produce very many prosoplasmas, the form and structure of the galls being very different and often very complicated.

The hemiptera also produce numerous, usually very simple prosoplasmas.

The hymenoptera produce almost entirely prosoplasmas, those produced by the gall wasps (Cynipida) are especially striking because of their size, the diversity and complexity of their forms and the difference in their internal structures. In describing the histology of prosoplasmas, we will have to examine especially thoroughly the structures occurring in Diptera and Cynipida galls.

Of the Coleoptera and Lepidoptera, only a few prosoplasmatic galls are known; their structure is relatively simple.

Among the Mycocecidia, there are various galls which resemble prosoplasmas in the regular arrangement of certain elements, for instance, of the cells of the membrane tissue which contain anthocyanin. Their cell forms, however, are no other than those which we are accustomed to meet with in arrested developments and in callus tissues. An especial position is taken by the gall, produced on Polygonum chinense by Ustilago Treubii[1]. This may perhaps be included among the prosoplasmas on account of its peculiar fibres which are like capillitia.

At least we may think that the transition from kataplasmas to prosoplasmas is furnished by the gall of Ustilago Treubii. According to Solms-Laubach, this fungus, like so many others, causes the production of canker-like excrescences here and there on polygonum stems. The excrescences consist of spongy, parenchymatous wood-tissue, on which account, this same fungus was referred to earlier (p. 196). These sprout out from the canker swellings which correspond entirely to the above described kataplasmas, "fleshy, succulent, easily breakable excrescences", "the irregularly bent, cylindrical and often longitudinally

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[1] Solms-Laubach in Ann. Jard. Botan. Buitenzorg, 1887, Vol. VI, p. 79.

(212) furrowed stalks of which are broadened at the top, like the head of a nail, and closed by flatly convex, smooth apical surfaces". The fungus forms its spores in this part of the excrescence - the "fruit-galls". These fruit-galls show a certain similarity to prosoplasmas (the size-proportions seem to vary); because of their characteristic form and still more in their peculiar differentiation. Such an one is produced by the outgrowth into long filaments of the cells of the host plant, lying at the fruiting spot of the fungus. Solms-Laubach compares these filaments, in their form and function, with the fibres of the myxomycetes-capillitia.

Still another fungus gall, closely related to prosoplasmatic galls, despite its simplicity, is that produced on the leaves of Potentilla Tormentilla by Synchytrium pilificum. Here and there are formed small, roundish, flat protuberences which are beset over and over again with very long, unicellular thick-walled hairs. All gall individuals are equally large and similarly formed. The small gall, which seems to be pretty rare, is of especial interest[1] because through it was illustrated the relations which were explained above, between constancy (and variability) of form and the constant (or changing) extent of the stimulatory
(213) field. The infecting organism does not extend beyond its nutritive cells; the field of stimulation is therefore always of uniform size. Also the developmental period of the parasite and the character of the stimulation varies in the Synchytriae within narrower limits than in many other fungi, which produces galls. Figure 80 explains the histology of the gall. In the centre is the nutritive cell, adjacent to it the parenchyma, and the epidermis with its many hairs, distinguished from normal ones by their size and the density of their growth.

In the following, we will first report on the external form and the course of development of the prosoplasmas and later investigate more closely the histological details of their development and the structure of the matured gall.

1. External Form and Course of Development of Prosoplasmas

The external form of galls varies greatly. In all cases they display extensive masses of tissue, which enclose a more or less spacious hollow cavity, in which the gall animals remain. While, in kataplasmas, the animal parasites live superficially or in cavities imperfectly closed, as in leaf roll galls, the prosoplasmatic galls are characterized by well enclosed cavities of definite form.

Prosoplasmas may be subdivided into four groups according to their form and course of development[2].

1. The simplest prosoplasmas are produced by the turning down or inrolling of the edge of the infected leaf. A leaf fold gall arises, which bears a marked similarity to many kataplasmas already named. A comparison of prosoplasmas and kata-

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[1] Thomas, Fr., Synchytrium pilificum, Ber. d. D. Bot. Ges. 1883, Bd. 1, p. 494. I owe the herbarium material to the kindness of Professor Thomas (Ohrdruf).

[2] Compare here Kerner Pflanzenleben, 1898, Bd. II.

plasmas acquires especial interest directly in the galls which are similarly formed. In contrast to those discussed above, the prosoplastic leaf-foldings are set off absolutely sharply from the healthy part of the leaf (galls of Pemphigus retroflexus and others on Pistacia). The characteristic crescent form of the gall is conspicuous in the products of Pemphigus semilunularius. Further, all galls produced by the same species are of the same size. Finally prosoplastic leaf-foldings, in contrast to those above mentioned, show a peculiar tissue differentiation. (Fig. 108 G.).

2. If, through the action of any gall poison whatever, a small part of the leaf-blade is stimulated to abnormally active surface growth, an outward curving of the leaf mass arises. Whether the curving in this is upward or downward depends upon whether the upper or the under side grows most intensively. Obviously the side which participates in the more active growth will become convex in the curling back of the leaf. The side growing most is always the one away from the gall animals; the one exposed directly to the irritation grows relatively little, so that, in this rolling of the infected leaf-area, the gall animals come to lie within the cavity thus produced. Figure 87 illustrates diagrammatically the production of this kind of leaf gall. The displaced part of the lamina is curved upwards and encloses, after further growth, a
(214) spacious cavity, which serves as a dwelling place for the gall animals. We term galls of this kind,- sac galls. It is evident that the cavities in which the gall animals here live can not be closed on all sides. An entrance pore always remains open. However, this can be extraordinarily narrowed by supplementary growth in thickness of the leaf-mass or may be stopped up by hairs.

In connection with sac galls we may also recall some earlier statements. Not a few forms are found among kataplasmas in which cavities are formed for the parasites by a curling and folding of the leaf. The same is true of many felt galls in which (compare above p. 115) hypertrophy of the epidermal cells combines with surface growth of the infected leaf, producing vesicular projections. In cases of this kind, however, the galls do not have the characteristic form and constant size proportions found in prosoplasmas. In them too the "sac" remains very primitive, in as much as the closing of the opening lying on the under side is either very incomplete or does not take place at all. Besides, in kataplastic sac galls new kinds of tissue forms never occur.

Sac-galls are produced especially by different kinds of mites, also by Hemiptera (leaf-lice) and Diptera (for instance, Cecidomyia bursaria on Glechoma). Their size varies greatly. The leaves of different maple species are often covered with small, reddish sac-galls, the smallest of which measures about 1/2 mm. in breadth. The galls of the aphis Tetraneura Ulmi, which lives on elms, become more than one centimeter large. The pale green sac of Schizoneura lanuginosa (on elms, compare fig. 54) becomes several centimeters large. The single galls are often spherical, as, for instance, the Phytotus galls on the maple. The well-known nail galls of the linden are slender and conical. Tetraneura Ulmi produces pocket-like galls, with slender bases and broad ends, Tetraneura compressa (on Ulmus effusa) coxcombelike sac-galls, Schizoneura lanuginosa often lobated and knobbed forms. Large sac galls, for instance, like those formed by Pemphigus marsupialis stand in isolated posi-
(215) tions on leaves (Populus) those of Tetraneura Ulmi and others are united into groups of a few galls, the small sacs of many

Phytopti (on Acer Negundo, Tilia etc.) not infrequently into groups of hundreds on the same leaf.

At times the folding of the growing leaf surface is more complicated than in the cases discussed as yet. Figure 82 illustrates a Phytoptus gall, occurring on leaves of Fragaria vesca. We often see below the sac a ring like fold, protruding from the underside of the leaf, by which the entrance pore into the sac-cavity is made smaller. At times these and other mite galls show further, often irregular complications in the folding of the leaf mass.

Sac galls similar to these found on leaves occur also - but much more rarely - on stalks and petioles. Under the influence of the gall stimuli, the bark tissue makes a strong surface growth, breaks away from the tissue layers lying more deeply and furnishes a tissue fold of definite form. Examples of galls of this kind are found in the branch gall produced by Phytoptus on Prunus Padus[1], as also in the epidermal fold galls which Thomas observed on Galium[2].

3. We will term the third class walled galls because of the nature of their production.

Walled galls of very different form and size are produced by Diptera, Hemiptera and Hymenoptera (Cynipides). During the production of the gall, the tissue lying directly beneath the gall animal, or rather the egg of the future gall-inhabitant, grows but little, if at all. The parts adjacent, on the contrary, grow out extraordinarly strongly. Figure 83 illustrates diagramatically the development of a walled gall. In a, the round egg is visible on the vegetative point of a bud. In b, the edges of the young gall may be recognized, which in c incline toward each other over the egg and in d are united.
(216) Galls of this kind can be produced on widely different parts of the plant, on vegetative points, on stems and stalks, on leaf blades and on roots. The processes of growth are always essentially the same, even when many eggs are deposited near one another and each one becomes walled separately. Figure 84 illustrates the production of the well-known bright red spring gall of Cynips terminalis on the tips of oak branches. Seven eggs are visible which were deposited near one another. A shows the first stage; at B-G the eggs, still partially provided with their long egg stalks, may be seen to disappear gradually in the outgrowing tissue. With Beverinck, we will term "gall plastein" the rapidly growing "embryonic" tissue, which the gall produces. In the finished gall its own larval cavity is reserved for each larva. While the developmental course shown in figure 83 led to a one-chambered gall, a multi-chambered form is produced in the manner illustrated in figure 84.

The "typical" walled galls here described are connected with the "typical" sac galls, moreover, by numerous transitional forms. Between the two stand the sac galls, which are provided with a so-called orifice wall such as are produced by various Phytopti and others. Figure 85A gives a cross section through the sac gall of Eriophyes similis (on Prunus spinosa) which originated in the leaf. The larger, upper part of the gall shows the sac produced by superficial growth of

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[1] Frank, loc. cit. p. 56.

[2] Aeltere u. neue Beob. ueber Phytoptocecidien. Zeitschr. ges. Naturwiss. 1877, Bd. XLIX, p. 351.

(217) the infected part of the leaf. On the entrance pore, however, we find besides this as a local outgrowth of the leaf-lamina, a ring-like tissue wall by means of which the entrance into the gall-cavity is considerably narrowed. According to Frank[1] this orifice-wall is produced earlier than the actual sac. Similar conditions exist in the case of the mite gall of Salix Caprea shown in figure 85B, only here the orifice-wall is extensive and fleshy, the sac remaining greatly below it in size. The gall animsls remain in the cavity enclosed by the "orifice wall",- they have been "walled in" by the outgrowing tissue of the leaf-lamina. Similar conditions also exist in the helmet-like beech-leaf gall of Hormomyia fagi (compare figure 58). Two developmental stages are illustrated in figure 86. The larva, remaining on the underside of the leaf, is "walled-in" (to the left in the figure), later the part of the leaf-lamina which lies above it makes an extraordinarily active growth in
(218) surface and thickness and furnishes the peaked, helmet-like part of the gall, which encloses an extensive larval cavity[2], (to the right in the figure). It is difficult to decide in cases like these described, whether a sac gall or a walled gall is present. However, we will not linger longer over this technical question of subdivision.

Even the "typical" unmistakable walled galls, in the production of which no sac formation comes into question, vary greatly among themselves. The external form as well as the nature of the closing of the entrance pore makes possible the recognition of many variants. Not infrequently the surrounding walls grow together and complete the closing of the larval cavity, (many Cynipides galls) in others the edges of the roll remain free (many Diptera galls); - to be sure, they lie close upon one another, but do not grow together. Anatomical structures of especial kinds may at times produce a firm cogging of the contact surfaces. In their outer forms, the walled galls often resemble spherical, wart-like, or egg-shaped bodies, or conical and bottle-like structures. The latter occur frequently among the products of the Hemiptera (for instance Pemphigus bursarius) and of the Diptera (Cecidomyia Corni and others).

Walled galls which, in their production, vary somewhat from the type described, are not rare and are often represented in our nature flora. Among the most striking of these belongs the spirally twisted petiole gall of Pemphigus spirothece, which often extensively deforms the foliage of poplar trees. At the infected points, the petioles grow out into fleshy, broad bands, which twist spirally and finally touch one another on their edges. The contact is so close that a lodging cavity, well enclosed on all sides, is formed for the animals which produce the galls, although no coalescence takes place.

Finally, the beech leaf gall of Hormomyia piligera deserves a special description. While, in the case of the sac
(219) and walled galls described above, we have taken it for granted that tissues lying above the infected place - epidermis, bark- even mesophyll - can be incited to (at least approximately) equal intensive growth, we now find in leaves infected by Hormonyia piligera that the upper epidermis can not participate

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1 Krankh. d. Pfl., 2. Aufl., 1896, Bd. III, p. 54.

2 Concerning developmental history see especially Büsgen, Zur.Biol. d. Galle v. Hormomyia fagi. Forstl.-Naturwiss. Zeitschr., 1895, Bd. V, p. 9 and Appel, Ueber Phyto-und Zoomorphosen. Würzburger Dissertation (Königsberg 1899).

in the growth. It is therefore ruptured by the strongly proliferating mesophyll, and a gall is produced, the outer covering of which - just as that of side roots produced endogenously or the like - does not originafe developmentally from that of the normal organ. Figure 87 illustrates a very young developmental stage of the gall. On the underside are visible the broad walled edges, by which the larval chamber has been formed; on the upperside, through active growth of a circular roll (aa), the epidermis (e) has been pushed up and ruptured. Under the covering thus pushed back, a flat tissue head, thickly beset with hairs, is produced, through the intensive growth of which the old epidermis already ruptured will later be stripped back and torn off. The greater mass of the nature gall may be traced back to this medial tissue head. With Küstenmacher[1], we will term "free galls" those which, like the ones here describbd, are not enclosed by normal tissue, or rather, its derivatives, but by a newly formed membrane-tissue. We will return to these in the next section.

4. While, in the forms as yet discussed, the gall animals persistently remained on the upper surface of the plant organ which produced the gall, or only later, by coalescence of the wall rolls, were enclosed on all sides by tissue masses; - we find in the representatives of the fourth group, that the entire development of the gall animal from the very beginning is enacted in the interior of the organs, bearing the gall.

If the eggs of the future gall-inhabitants are deposited by the mother animal in the interior of any plant organ whatever and the infected tissues are stimulated to outgrowth, <u>cambial galls</u> are produced. Representatives of this fourth type are found among Diptera and Hymenoptera galls.

While in sac galls the abnormal growth took place predominantly parallel to the upper surface of the infected plant organs and in walled galls the direction of growth was so determined by the egg and the larval body, that the tissue increased most actively tangentically, we can call the radial direction the one preferred in the growth of cambial galls. Round about the larvae or the eggs a large tissue knot is produced, of a spherical, egg-shaped or elliptical form, which appears as a thickening of the infected stem, or as an embossment of the infected leaf, or may be attached to the leaf, stem, root etc. as an independent appendage, while the outlines of the organ which bears the gall would not be essentially altered by it. With <u>Lacaza-Duthiers</u>[2] we can call the first kind internal galls, the second kind external ones. That numerous transitional
(220) forms are found is directly evident. Further, we will have to distinguish between one and several-chambered galls, as in walled galls.- For instance, the galls produced on Salix by nematode species (leaf wasps) contain only one chamber (compare for example figure 88). The large stem knot galls of <u>Aulax Hieracii</u> on various species of hawk-weed are many chambered.

Further, the difference between "free" and "enclosed" galls (Küstenmacher) deserves especial consideration. In cambial galls it frequently happens that only the tissues which lie in the closest proximity to the egg can increase abundantly,- the cell layers lying above participating little or not at all in the outgrowth. The inactive tissues are ruptured by those

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[1] Loc. cit. p. 112.

[2] Rech. pour servir a l'histoire d. galles. Ann. Sc. Nat. Bot., III serie, 1853, T. XIX, p. 273.

growing so strongly and the new formation pushes outward. While in the cambial gall of a Nematode shown in figure 88, the epidermis persistently surrounds the luxuriant tissue excrescence, we find in other galls that the covering tissue holds its own only at the beginning so that in the end tears are formed, in which the more deeply-lying gall-tissue is exposed. The galls of Aulax Hieracii, Lasioptera and others are "enclosed" by a moderate development of the gall-excrescence. In the case of especially luxuriantly developed specimens, however, the normal covering tissue is ruptured here and there and the formation of wound cork is eventually necessary. In many Cynipides galls (in the autumnal galls of Neuroterus lenticularis n. numismatis etc.) from the very beginning only a small tissue complex in the interior of the organ, producing the gall, is capable of increasing, "gall-plastem"). The outgrowth progresses rapidly, breaks through the inactive outer tissue layers and develops its own covering tissue,- just as the "free" walled galls of Hormomyia piligera are formed (see above, figure 87). Figure 89 shows in cross-section the free cambial gall of Biorrhiza aptera (the winter generation of the above-named Cynips terminalis) which abounds on the roots and young branches of Quercus. The endogenous origin is made clear by the drawing, without further explanation.

(221) The manner of production of "free" galls necessitates the fact that they usually appear as more or less independent appendages of the plant organ bearing the gall. However, it would be absolutely unjustifiable to wish to draw conclusions from the external appearances of a mature gall as to the ontogeny of this gall, which, like that of Biorrhiza aptera, rests like an independent organ upon its substratum. Thus, for example, the gall apple, produced by Spathegaster baccarum (on Quercus inflorescences and leaves) as a walled gall, covered round about by derivatives of the normal epidermis, and the dainty gall-apple of Nematus gallarum (on willow leaves), disregarding its morphologic independence, are cambial galls with the same development as the one shown in figure 88.

The description of the much ruptured gall of Lasioptera picta, or of Aulax Hieracii proves further that no sharp boundary may be drawn between free and enclosed galls. I would like finally to mention one more type of cambial gall, in which, as in the case of the walled gall of Hormomyia piligera, regularly defined portions of the new formation remain covered by the normal epidermis, while others become exposed. In figure 90 is shown a cross-section through an otherwise undetermined (Diptera?) gall from the leaves of Parinarium obtusifolium (Chrysobalanes) which will interest[1] us in many ways. In it a short, cylindrical gall is produced by a local outgrowth of the mesophyll. Thus the strongly proliferating portion of the tissue ruptures the epidermis which lies above it and, by growing further, elevates it. Similar processes are repeated on the opposite side. We find here a tissue ring increasing relatively weakly, in the development of which a circular rupture is formed, the medial field of the epidermis remaining at its original
(222) level while the adjacent parts are raised by the outgrowing tissue ring. However, no new, real epidermal tissue is produced on the exposed parts. I know also of similar processes in other galls.

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[1] Unfortunately, only herbarium material of this interesting gall was at my disposal. (Herbar. Monacense).

I would like to call attention to the fact that the formation of "free" galls is not met with in prosoplasmas alone. If, by the action of Schizoneura lanigera (compare above p. 205), a kataplasmatic woody-excrescence is produced, which distends the bark and then splits it, the developmental process is evidently similar here to the prosoplasmas just described. Also, other stimuli besides gall stimuli can call forth similarly outgrowing, endogenous formations. In the intumescences illustrated in figure 20, only the mesophyll increases in this way, finally rupturing the epidermis.

Further reference should be made to the fact that the developmental difference, proved between walled galls and medullary galls, is expressed also in the gall products, which arise only through growth of the cells without subsequent division (gall-hypertrophy). In Erineum galls, the gall animals are "walled in" more or less completely by the growing epidermal cells. In the vesicle gall occurring often on Viburnum Lantana (figure 43) a typical medullary gall is produced by growth of the ground tissue cells.

The forms of the various medullary galls differ greatly. The elliptical is most frequently repeated. Where leaf galls are concerned, the gall is either visible on both sides of the leaf as calotte-like swellings (figure 88) or it is attached on one side by a small, thin stalk. In the former case, either both sides are equally or approximately equally developed, as, for instance, in the gall of Nematus vesicator, N. Vallisnerii etc., or there is present a decided dorso-ventrality (compare figures 111 and 112). The upperside displays a different form from that of the under side. Not infrequently, the dissimilarity between the upper and under sides may be recognized only by considering the anatomical conditions (figures 108 and 93). Next to the elliptical, the spherical form is usual. (Nematus gallarum etc.). More complicated forms with diverse outgrowths, constructions etc. may be found among the Cynipides galls.

Although the prosoplasmas have a peculiar characteristic form, small variations, corresponding to external conditions, are not rare. It seems a matter of course that the form of the gall varies from the usual one, if unfavorable spacial conditions arrest its development;- this case abounds in those galls which are developed in a small space, in closely congested groups (Neuroterus lenticularis etc.) and are thereby united into extensive masses (Cecidomyia Corni).

Still more interesting is the fact that many of the galls, capable of developing on different organs, assume different forms on different substrata. However, in all the cases known to me, this formal difference is very unessential.
(223) Diplosis botularia can infect different parts of Fraxinus leaves. If the midribs of the leaflets are infected, roll-like leaf-foldings are produced, as shown in figure 91A. But if the galls are formed in the leaf axis, the slender leaf-blades of the rhachies swell out into fleshy ridges, which enclose the larvae cavity (figure 91B). The majority of the other gall animsla, however, (Diplosis tiliarum, Spathegaster baccarum etc.) which form their galls on different organs of the host plant, always produce the same gall form - with but very slight differences.

The oft-quoted statement that Rhinocola speciosa produces other galls on the leaves of a species of poplar in Germany than it does in Aragon[1] needs more exact proof. Besides, in the gall productions of Rhinocola, kataplasmas are probably the ones concerned.

I have already called attention to the fact that the external and internal peculiarities of prosoplasmatic galls may be traced back indeed to the quality of the gall stimulus and the composition of the gall poison given out by the parasite, while the constancy of the proportions of size and form cannot be explained so well by the quality of the infection as by the extent of its action and its type. In prosoplasmas, gall animals are involved, which cannot at will leave or change the place infected as can possibly be done by wandering leaf-lice etc. nor can they extend it irregularly, or indefinitely, as do outgrowing fungi, only a narrowly limited field of infection is produced. Further, the poison causing a production of the gall is introduced into the plant only once with the deposition of the egg - or it is effective for a comparatively short time - thus the period of stimulation is evidently very limited. Like this, the development of the gall soon ends. Although the galls of the Gymnosporangia etc. continue growth for years, never reaching any real final or "mature" stage, prosoplasmas reach
(224) their last phase of development a few days or weeks after the deposition of the eggs, corresponding to the rapid developmental progress of the parasites.

In speaking of a limited period of stimulation, we think indeed only of the most important of the stimuli, to whose action the tissues which produce the gall and the gall itself are exposed; i. e. of the chemical stimuli arising from the gall poison. However, for at least some prosoplasmas, it has become evident that another kind of stimuli co-operates in their production and formation - wound-stimuli. Either the gall mother injures the plant organ, before she deposits her egg, thereby causing the production of callus tissue, or the growing occupants of the gall gnaw its tissue. In the present consideration, the second is the more important case, because there exist in it stimuli of long continued, ever repeated action. We find that the tissue of the galls responds to the stimulus of injury with the same reaction as wound normal tissue. Callus hypertrophies are produced (in the elliptical galls of the Cynipides infecting oaks; see below p. 254), or callus hyperplasias (as in the galls of Nematus vallisnerii) the formation of which can be continued long after the form and size of the gall have reached their last stage; the important external characteristics of the gall are not influenced by these supplementary, long continued phenomena of growth. In kataplasmas, on the contrary, the chief role is played by wound stimuli and by those of gnawing which proceed uninterruptedly from the producers of the gall. Their effect is determinative for all the qualities of the gall and the assumption is a propos, that possibly in many cases, no other stimuli are effective.

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1 According to Eckstein, Pflanzengallen u. Gallentiere. Leipzig, 1891.

Since we now understand clearly the external form of the different species of galls, so far as of interest here, we will now turn to the results of microscopic research; we will first look more closely into the life history of the galls and then investigate the different kinds of tissues in mature ones.

If we study the abnormal cell-divisions which usher in the formation of the galls, we can distinguish three types, according to their direction; a regular orientation of the cross-walls can not be recognized in young galls, or the cells divide predominantly perpendicular to the upper surface of the organ involved, or they divide chiefly or exclusively parallel to the surface of the organ.

The galls of Cynips terminalis which consist of irregular callus tissue (compare fig. 84) furnish an example for the first case in which all regular orientation of the cross-walls is absent in the young galls. No definite direction of cell-division may be found in the young walling-in rolls.

We find division predominently perpendicular to the upper surface of the organ which bears the gall in the galls produced (225) by growth parallel to this surface;- in sac galls. In investigating early stages of development, cell rows are often found running tangentially which have originated from one cell by anticlinal division. Figure 92 illustrates this case by a cross-section through the gall of Pemphigus marsupialis (on poplar leaves). In most sac galls, numerous periclinical divisions are added to anticlinical ones; However, the galls of Cecidomyia bursaria (on Glechoma) for example, seem to be produced practically exclusively by anticlinial walls. At least in the examples which I have investigated, I could find only here and there an isolated periclinial wall.

Most medullary galls may be traced back to divisions parallel to the upper surface of the organ which bears the gall. Instances are not rare here, in which extensive galls are produced exclusively by cell division in one direction. Even in mature, ripe specimens at times the regular arrangement of the cells in rows leaves no doubt on this subject. Figure 93 shows part of a cross-section through an undetermined (Diptera?) gall of Banisteria[1]. Leaving the epidermis and upper palisade layer of the mesophyll (P) out of the question, all the cells of the leaf tissue have divided extraordinarily actively and have produced long, strikingly regular cell rows. Cell division does not always take place equally intensively in all parts of the gall, rather, it is strongest in the middle and weakest at the edges. In this way, many flat elliptical galls are produced on leaves (Cecidomyia tiliacea on Tilia, Hormonyia Caprea on Salix Caprea etc.). In cross-section, the cells are found to be arranged in regular rows, which, running in straight lines at the center, are rolled up at theedges, turning their concavity toward the periphery (compare fig. 94); the cell rows and the outlines of the gall may be considered a system of orthogonic trajectories.

(226) The distinction between galls produced predominantly by anticlimal division and those others produced entirely by periclinal division still has an especial significance, in so far that the histology of galls of the first kind always remains simple, while in the others, besides simple structural conditions, extraordinarily complicated ones also may be found.

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[1] From the herbarium in Munich.

Also, the external form of the galls very often does not make possible conclusions as to the kind of cell division, by which they are produced. Figure 95 shows a very early stage of the walled gall of Pemphigus bursarius, which is active on the stems of poplar leaves. In cross section through the tissue ring (fig. 95B) a higher magnification shows that the cells of the bark parenchyma, together with those of the epidermis, have been much divided anticlinally. Near these may also be found periclinal walls, which are greatly increased during the further development of the gall. Figure 87 illustrates a young gall of Hormomyia piligera. Here too a similar tissue ring (a-a) has been developed, which is ;roduced, however, merely by division of the mesophyll cells, parallel to the leaf surface. It is hard to prove isolated anticlinal walls here and there in the tissue.

(227) The question as to the tissue material, used in the formation of galls, may be considered from several points of view.

Thomas has thoroughly tested the tissues of plants which produce galls, as to whether they are capable in all stages of life of reacting to the gall stimuli by cell division. His investigations proved that only those tissues are able to form galls which are attacked during development[1]. In other words, permanent tissue is incapable of forming galls.

First of all, to keep to prosoplasmas, no case is known, in which permanent tissue had served as material for the formation of galls. This result is surprising in so far, that in other pathological tissues, even the cells of permanent tissue are found to react to stimuli of different kinds with most diverse phenomena of growth. I will call attention only to the formation of callus from bark parenchyma which is several years old and from medullary tissue,- to the production of callus on old "ripened" Begonia leaves to the hypertrophy of the bark of
(228) Gold-ribes, to the formation of tyloses in old wood etc. But what is the condition in kataplasmas, for example, in the bark gall, of the beech-wood louse (Chermes fagi)?. Hartig's investigations (see above p. 207) prove that, in small trunks which are several yeard old, the bark cells are incifed to proliferation and that the formation of galls can extend even into the wood; thus here old tissue,- permanent tissue- can obviously be brought to excrescence and used for the formation of galls.

However, it has been emphasized above, that these very galls of the beech woolly louse (compare fig. 79) possess the greatest similarity to callus tissue. Therefore, the question must be asked, are only wound stimuli concerned in the formation of the beech-Chermes-gall, by means of which the permanent tissues can be incited to the formation of callus, in the same way as perhaps by girdling, or other somewhat coarse attacks? And further, may the permanent tissues be distinguished from those which have been attacked during development by the fact that they can react with cell division to wound and many other stimuli but not to chemical ones? I consider it very improbable that a pos-

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[1] Compare Thomas, Zur Entstehung der Milbengallen u. verwandter Pflanzenauswüchse. Bot. Ztg., 1872, Bd. XXX, p. 284, Beob. ueber Mückengallen, Programm Gympas. Ohrdruf, 1892. Other investigators arrived at the same results. Compare Sachs, Physiol. Notizen, 1898, p. 84 (also Flora, 1893, Bd. LXXVI, p. 241). Beyerinck, Beob. ueb. d. ersten Entwickelungsphasen etc. loc. cit. p. 180. Appel, loc. cit. p. 52. For the older point of view, compare also Hofmeister, Allg. Morph. d. Gew., 1867, p. 634.

itive answer can ever be given to the second question: There is no reason for surmising any such difference in principle between mature and immature tissues, between chemical and "traumatic" stimuli. It would be quite another question, as to whether the chemical stuffs, furnished by the gall-producing parasites, are the ones suitable for inciting the cells of permanent tissues to division.

It seems to me that a further point must not be overlooked here. If prosoplasmas are produced only from tissues attacked during development, the explanation may lie in the unfitness for use of the permanent tissue, but may also be based,- in some or in many cases,- on the fact alone that the gall animals give out their poison only to young organs and avoid the old parts. Whether the permanent tissues may perhaps be able to proliferate, when it is possible to carry through infection in them, is a question for the solution of which naturally experimentation is necessary. Unfortunately, however, as is well known, all attempts with experimental cecidiology have failed, up to the present. All my efforts to influence Phytoptes to colonization and to cause them to form galls on permanent tissue have miscarried. Still, I do not give up hope of coming to positive results in later series of experiments. Perhaps it is advisable to make use of organs, whose tissues are mature, but have also remained tender, so far as their cuticula etc. are concerned. I plan at some later opportunity to take up again my experiments with etiolated plants or with specimens from moist cultures.

Many galls are produced from completely undifferentiated tissue, from the primary meristem of the tips of shoots or from callus tissue. Many others are produced from organs whose tissues already show some distinct differentiation. It is now necessary to make investigations as to whether all tissue-forms of the host plant can furnish material for prosoplasmatic outgrowths and further, whether all participate to the same amount and in the same way in the production of the tissue outgrowths[1].

(229) From the outset, cells and tissues with lignified walls are excluded, since, as is well-known, they can not make any further surface-growth. As for the rest, all living cells can, under certain circumstances, participate in the formation of galls - no matter if they belong to the epidermis, the ground tissue or the vascular bundle tissue.

In stem-galls the vascular bundle tissue and especially the cambium belonging to it, often participate greatly in their formation. Indeed, many galls of the Cynipides winter forms are produced exclusively from the vascular bundle tissue (compare fig. 89). In leaf galls the activity of the vascular bundles is less, and often no increase of its cells may be noticed,- rather their development is often prematurely arrested.

In most cases, the ground tissue produces the largest mass of galls; pith, bark, and mesophyll often proliferating with astonishing luxuriance. If, in leaf-galls, the infected part of the leaf attains ten or twelve times the thickness of the normal leaf, in almost all cases it is the mesophyll along which has been active. Figure 96 gives a cross-section through the edge of a gall of Cecidomyia tiliacea. Not only the cells of the assimilatory tissue have been enlarged and strongly increased, but even the colorless ground tissue cells, which con-

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1 Compare Küster, Cecidiolog. Notizen. Flora, 1902, Bd. XC, p: 67.

(230) nect the transverse ribs with the epidermis on top and underneath. On the other hand, cases are not lacking in which all parts of the ground tissue of the leaf can not increase in the same way. In many fungus galls, the spongy parenchyma is superior to the palisade tissue in its capacity for increase. The same difference is evident in many zoocecidia; of a prosoplasmatic character. Figure 93 illustrates a (Diptera?) gall of Banisteria, in which the uppermost palisade layer has remained inactive, while those lying deeper have divided repeatedly.

The epidermis always participates only moderately in the formation of galls. Very often its cells, in contract to those of the mesophyll lying directly beneath them, do not divide at all; for instance, in the gall of Hormonyia piligera (compare fig. 87) the growth remains less than that of the more deeply lying tissue-layers, so that the epidermis is ultimately ruptured. In the sac gall of Tetraneura Ulmi the inner epidermis, lining the cavity of the gall, is not able to keep pace with the growth of the outer epidermis and most of the ground tissue layers; its cells are usually distended, drawn out to "retort" cells with thread-like necks, and finally torn apart (compare fig. 97). The cells of the adjacent mesophyll layers act in places like this under epidermis. Instances of this kind, however, are rare. Sac galls and walled galls are usually covered with an uninterrupted epidermis, of which only the superifical growth has been active.

Epidermal growth in thickness is very much rarer in galls. To be sure isolated cross-divisions occur in many galls (Urtica, Tilia fig. 96, Juglans (Küster, loc. cit.), but only rarely a many-layered epidermis from a single-layered one. The galls of Spathegaster baccarum can be taken as examples, also the flask-like fly-galls of the elm (fig. 99) and especially the abundant willow galls of Nematus gallarum. (Figure 98). In these, a sheath of tissue of varying size is formed from the thin epidermis; at H. in figure 98, the epidermal tissue seems to be constricted, since no division in the hair cell has taken place at that point.

I have already called attention to the fact that no conclusions as to the participation of the different tissue-forms in the construction of the galls can be drawn from the nature of the host plants and their normal histogenetic peculiarities. In the Salix species, the cork is known to be produced from the
(231) epidermis. As we have found, the epidermis in many willow galls is many layered. To conclude from this that the epidermis of Salix is especially inclined to cross-division would be absolutely useless. Willow galls (Phytoptocecidia) may be found, in the production of which the epidermal cells remain undivided. On the other hand, in the elm galls above named, we have found that the epidermal cells divide extraordinarily actively, which does not take place under normal conditions and that in Ulmus the cork is produced sub-epidermally - and the like.

Galls have often been compared to tumors or swellings of the animal and human body. In fact, in one as in the other, a diseased new formation of tissue is involved, which shows a moderate similarity in external form in all. Further, in both cases, a similar connection exists between outgrowth and substratum. In galls also, we may speak of "malignancy"; since they often take appreciable amounts of food stuffs from the ground tissue, in this, resembling tumors which, like parasites, use up their substratum and entirely exhaust it. Besides this very little correspondence can be proved.

Fortunately we are able in galls to investigate exactly their first developmental stages; the organic connection be-
(232) tween the pathological new formations and the ground tissue has been cleared up beyond all doubt. Phenomena, explained only by a deposition of germs, are suppressed from the very beginning. Galls, in contrast to tumors,[1] are developed by a typical infection growth; the stimulus which incites normal cells to proliferation can often be transmitted very far and can cause active hyperplastic growth even at a considerable distance from the original place of infection. Galls enlarging by infiltration, are not known as yet[2].

Tumors consist principally of connective tissue, but some of connective tissue and epithelium, or connective tissue and fatty tissue and the like; we will leave the blood vessels out of this discussion. In plants, the ground tissue is as significant in the formation of diseased outgrowths as is connective tissue in tumors. "Mixed swellings" occur very frequently in galls, epidermal outgrowths and those of the bark, or rather the mesophyll, uniting and forming an homogeneous whole. Thus we can prove at the same time that in galls arising endogenously the fundamental tissue of the plants can develop typical epidermis (with lenticels, hairs, etc.) on its upper surface and that the cells of this epidermis can produce derivatives in every way resembling the cells of the ground tissue, which in the mature galls are no longer distinguishable from the descendants of normal ground tissue. Therefore, we cannot speak of a "specificity" of the epidermis etc. in plants, in the sense that, in abnormal outgrowths, only new epidermal cells will be furnished by the epidermis and that no epidermis can be produced from the fundamental tissue. As is well known in animal tissues, such a difference between epithelial and cambial tissue as here described is accepted as certain by most histologists.

The histological structure of tumors even im "mixed" swellings" may be characterized as very simple, when compared with the higher organized prosoplasmas. No tumor is known, which consists of characteristic tissue zones of such diversity as those of the gall products of the Cynipides, the Diptera etc. Rather, in many tumors, the production of but slightly differentiated cells may be confirmed. In this, tumors correspond to callus tissues and galls termed kataplasmas. In common with these, tumors may also have the negative characteristic that they have no definite external form nor definite size proportions. In many tumors, as in many kataplasmas, we may speak of theoretically unlimited growth.

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[1] Compare especially Ribbert, Lehrb. d. Allgem. Pathol. Leipzig, 1901.

[2] Infiltration growth often occurs elsewhere in the developmental history of plant tissues. The parasitic fungi, the "thallus" of the Rafflesiaceae, the haustoria of many phanerogamic parasites, grow infiltratingly on their substratum; infiltration growth occurs also, for example, in unbranched latex tubes and pollen tubes, the haustoria of embryo sacs and others. I have never been able to observe that galls develop forms like haustoria at their bases; future investigations, however, may perhaps make known phenomena of this kind.

As said above, the histology of prosoplasmas[1] furnishs their most important characteristics. In regard to tissue dif-
(233) ferentiation, prosoplasmas do not have the character of arrestment forms, but consist of tissue newly differentiated and usually differing strikingly from the normal ones of the ground tissue and often greatly exceeding these in the abundance of their cell forms etc.

Prosoplasmas differ among themselves ax greatly in regard to structure as to external form. Besides highly complicated forms composed of three, four or five kinds of easily distinguishable tissue forms, simple ones may be found which also furnish histologically a transition to kataplasmas; the larger galls especially do not display in all parts structures varying as above mentioned, from those of the ground tissue. Not infrequently only the inner parts are formed with a prosoplasmic histological character, the peripheral ones resembling kataplasmas.

A concentric structure is common to all prosoplasmas. No matter if roll-galls, sac, walled or medullary galls are concerned, we find that as soon as several different tissue layers have been formed, they surround the larval cavity as concentric layers. Further, the innermost zone is always formed of a delicate tissue material and the outermost of a very firm one. In the simplest cases, only one epidermal layer, provided with a firm cuticula, represents this "firm" tissue; in cases structurally more complicated a peculiar layer may be found, constructed of sclerotic elements, or indeed several such layers. The inner soft part of the tissue;- for instance, in sac galls,- is formed of delicately walled epidermal cells and those of the adjacent ground tissue, which are richly filled with albumen and starch. In medullary galls, the innermost layers, bordering the larval cavity, are, as a rule, delicately walled and rich in cytoplastic substances. Tissues of this kind just named give the galls the solidity necessary for their occupants, the others furnish the food necessary for the parasites. Almost all tissues, composing prosoplasmas serve one or the other "purpose",- all others fall far behind them. Protective tissue and nutritive tissue are not only universally distributed and make up the chief mass of most falls, but also have in the different forms so diverse a formation, that we must devote a detailed consideration to them.

In this histological treatment, as above in the discussion of external forms, we can affirm that the same characteristics found in prosoplasmas may also be proved in the very much simpler gall-hypertrophies (p. 107). In many Erineum galls a protecting layer is brought about in a very

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[1] Statements in the histology of galls are to be found abundantly in cecidiological literature. As comprehensive works, only the following come under our consideration: Lacaze-Duthiers, Rech. pour servir a l'histoire d. galles. Ann. Sc. Nat. Bot. 3me ser., 1853, T. XIX, p. 273. Beverinck, Beob. ueb. d. ersten Entwickelungsphasen einiger Cynipidengallen. Amsterdam 1882. Küstenmacher, Beitr. z. Kenntn. d. Gallenbildungen, etc. Pringsheim's Jahrb. f. wiss. Bot., 1895, Bd. XXVI, p. 82. Fockeu, Rech. anat. s. l. galles. Lille, 1896, (compare also Rech. s. quelqu. galles foliaires. Rev. gen. Bot., 1896, T. VIII, p. 491). Appel, Ueb. Phyto - u. Zoomorphosen. Königsberg. 1899. Küster, Beitr. z. Anat. d. Gallen. Flora, 1900, Bd. LXXXVII, p. 117 and Ueber einige wichtige Fragen d. Pathol. Pflanzenanat. Biolog. Cbl. 1900, Bd. XX, p. 529.

(234) striking way by means of the growing together of the club-like ends of the hairs and the thickening of the outer membraneous parts; the nutritive tissue at any rate being furnished by the hairs, the filling of which with starch oil etc. was discussed above. The bladder galls of Viburnum Lantana are for the most part composed of nutritive tissue (compare p. 119).

Besides the differences separating kataplasmas from prosoplasmas, some characteristics common for all galls should be mentioned.

Above all, the tendency to form parenchyma is striking; the galls are almost entirely parenchymatic structures. To be sure, ducts may be found in them, but these ducts themselves are composed of parenchymatic elements. The lack of libriform fibres in all gall formations, even the most highly organized, is very noticeable[1]. In these negative characteristics, the prosoplasmas conform to callus tissues, wound wood and kataplasmatic galls.

Further, the suppressed retrogression in the formation of tracheal elements is conspicuous; galls generally contain only very scanty vascular bundles, the ducts usually having narrow lumina. Similar conditions are found in kataplasmas, where the production of parenchyma also retards the formation of tracheal cell-forms.

The same is true of the scanty chlorophyll content of galls. They are as pale a green as many fungus galls, most callus tissues, etc. In many the green pigment is entirely lacking.

We will herewith pass over to the discussion of the different kinds of tissue forms in galls and will begin with the two most important, the protective and nutritive tissues. As less inportant, the sparsely developed fibro-vascular, the assimilatory tissue and a few others will be named later.

1. PROTECTIVE TISSUES

As the protective tissues of prosoplasmas, there come under consideration, the covering tissues and, also, especial complexes of stone cells. We will term the latter mechanical tissue. No absolutely sharp line can be drawn between both forms of protective tissue because many peripheric cell layers in galls, including the epidermis, are often composed of similar elements, resembling stone cells.

Epidermal Tissue

At this point, the epidermis comes under our consideration, only in so far as it performs the functions of a covering tissue and, by means of an unbroken covering, a strong cuticle or because the production of hairs gives protection to the more deeply lying tissues. The epidermis in sac and walled galls, which lines the cavity of the gall, has other functions and will be discussed later. Further, we will have to discuss
(235) only those forms of epidermal tissues which in gall-production are not carried over in an unchanged form from the normal parts of the plant, bearing the galls, as is the case in many medullary galls, but which in some way vary from the normal in their

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[1] Compare here statements on p. 246 on the gall of Synophrus.

histology. For the present consideration, it is immaterial whether the epidermis of a gall is derived developmentally from the normal one, as in "enclosed" galls, or is to be concrived of as a new formation, as in "free" galls.

In sac and walled-galls the outer epidermis is composed mostly of relatively large, but often very flat cells, which are provided with only a moderately strong cuticle. At times, a many layered epidermis can be formed from one which, under normal conditions, would have only one layer. Isolated cross-divisions may be found in various galls (see above), but such a mighty epidermal sheet as that found in the Diptera gall on Ulmus[1] shown in figure 99 is rarely produced. Here and there eight, ten and more epidermal cells lie on top of one another.

The external galls (Lacaza-Duthiers galles externes) which appear attached as special appendages to the organs bearing them, at times produce as many layered epidermis and often show a strong cuticle on their outer walls. In the ("enclosed") gall of Nematus gallarum, the cells are rather small and strongly cuticularized, (compare figure 100A), in the gall of Andricus quadrilineatus they are distended like papillae and have rather thick walls. (Fig. 100B). In a Californian Cynipides gall on Quercus Wislizeni, the outer walls of the epidermal cells and the upper part of the side walls are thickened, so that an approximately conical cell-lumen remains free (compare fig. 114). The gall of Acraspis macropterae (figure 106) has thick-walled epidermal cells, with at times a pit-like wall structure.

I found a very singular epidermis in a gall of Jacquinia Schliedeana Mez. The inflorescence stalks swelled out to thick, turnip-like bodies, the covering tissue of which is shown in figure 101. The cells in the outermost layer con not, for any length of time follow the gall's continuous growth; they are pressed into sheets, their walls are constantly drawn out thinner and finally tear apart. At the same time, the cells of the layer lying immediately beneath this one assume the func-
(236) tions of the epidermal tissue, since their outer walls are greatly thickened and powderfully cuticularized. Even the third and fourth cell layers can be transformed in this way. In the figure at a. is shown the overlapping of the wall-thickening and of the process of cuticularization in the cells[2] lying deeper.

So far as I know, cork as a covering tissue is one of the rarities in galls. It is formed comparatively luxuriantly in the gall of Neuroterus numismatis (On Quercus), the characteristic form of which is shown in figure 102a. In the central depression on the dorsal part of the gall are formed several

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[1] Schlechtendal's Verzeichnis, Nr. 361.

[2] So far as my slight tests permit of a decision, a similar epidermal substitution does not take place on normal axillary parts of Jacquinia Schiedeana. Sclerâder (System. Anat. d. Dikotyl., p. 577) mentioned a subepidermal formation of cork in Jacquinia. Damm has announced recently that the cells of the bark parenchyma in various plants form cuticular layers and cause the production of a "cuticular epithelium" (Ueb. d. „Bau. die Entwickelungsgesch. u. d. mechan. Eigenschaften mehrjähr. Epidermen bei d. Dikotyl. Beih. z. Bot. Cbl. 1901, Bd. XI, p. 219. Cuticular epithelium may be proved in various Viscoideae. A new example is illustrated by the gall treated of in the text.

layers of thin-walled cork. Wound-cork is occasionally met with in these galls, in which the outer layers are ruptured by the intensive growth of the inner ones (for instance, in galls of Aulex Hieracii[1], Lasioptera.

The formation of bark is known as yet only in a few galls (Aptera and Radicis galls). (Beverinck loc. cit. p. 64).

Trichomes, which in structure and arrangement, may well serve as a protection to the covering tissue in its functions,
(237) are not unusual in prosoplasmas. The gall of Nematus bellus (on Salix) bears a thick covering of hair, as do those of Hormomyia piligera (figure 87) and Neuroterus lanuginosus. The oak galls of Neuroterus lenticularis and N. numismatis bear hairs of a striking form. Star-like bunches of hairs are found on the former, the single components of which are thick-walled and filled with a brown content; in the others, we find a thick silky hair covering round about the edge of the gall (Figure 102a). The hairs of the lenticularis gall are interesting since the bunches of hairs of this stiff, short-membered form are found on numerous Quercus varieties, but not on our native ones. The hairy forms of the numismatis gall occur neither on the German nor on any other Quercus variety. They are long, unicellular, sharply pointed and often two-armed. Both arms differ greatly in length (compare 102c) and are always so oriented, that the longer of the two seems to be centrifugally directed, the shorter turned toward the central point of the upper side (at a). When studying cross-sections, one cannot suppress the thought that spacial conditions regulate predominantly the production of the two-armed forms. To all appearances the hairs
(238) become two-armed, because they fill out the space at their disposal. At b in the figure, differently formed hairs are shown; some are bent sharply, like knees, another kind is bent twice and provided with a "shoulder" for a second arm. Forms of this kind and similar ones are produced only as a result of a lack of space[2].

By far the majority of prosoplasmas are naked or only slightly pubescent.

Many galls lack all covering tissue. The galls of Cynips terminalis on the tips of shoots, produced from callus-tissue, are made up externally of homogeneous parenchyma, the outermost layer not being characterized in any way as epidermis or cork, Moreover, the galls here mentioned belong to those, which "crack open" in places and expose their inner tissue. In others, the epidermis is lost inan early stage and is replaced by hypodermal layers of stone-cells.

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[1] Compare also Skrzipietz, P., Die Aulaxgallen auf Hieraciumarten. Dissert. Rostock, 1900.

[2] While I trace the branching of the hairs here described to the action of spacial conditions, I assume that even in single cells the same phenomena of "correlative growth" can take place, as in some organs (for instance, roots, compare above p. 140). I would like also to trace back to similar conditions the production of abnormally formed tracheids in the gnarls of wound-wood, especially the formation of branched forms. (Compare figure 70).

We will term mechanical tissues those which are composed of stone-cells. This name is justified by the fact that without doubt the layer of stone cells can act mechanically because of its firmness. The larval chambers, which are composed of mechanical tissues, and their inhabitants are thus shielded from pressure and blows - and protected from the attacks of animal enemies. Lacaze-Duthiers, who had recognized this community character of the stone-cell tissues in galls, termed the firm zone a "couche protectrice".

Compared with the formation of mechanical tissue in the normal plant body, the strengthening tissues of galls may be of two kinds: either the galls carry over their mechanical tissue from the plant organ, which produces them, or they produce a tissue of this kind for themselves. "A Pathological Anatomy" is naturally concerned only with a study of the latter.

The "external" galls only rarely lack all mechanical tissues as in the different nematus varieties on the willow. We find in most galls an extraordinarily rich production of stone-cell tissues. We will study first of all the qualities of the single, thick-walled cells and later the form and distribution of mechanical tissues.

1. All thick-walled cells, found in galls, are sclereids. Sclerenchyma fibres (stereids) are absolutely lacking in galls. The omission of the prosenchymatic mechanical elements conforms with the parenchymatic character peculiar to all gall tissues and also to callus formations.

Within the boundaries drawn for the forms of the mechanical cells by their strongly retained sclereid-character, we find nevertheless an abundant variation. The form of the stone cells
(239) differs greatly in the different galls; their porosity and the degree of lignification are also unequal. Finally, the stone cells are very noticeable, which are produced by the unequal growth in thickness of the cell-membranes.

In the majority of cases the stone cells of the galls are small, round, and iso-diametric, as shown in figure 93 (Banisteria gall). In other galls, however, we find angular cell forms, stretched like palisade-cells and usually oriented perpendicular to the upper surface of the gall body, similar to the rod-like sclereids of many fruit and seed shells. Figure 103 gives the cross-section of a gall of Hormomyia fagi. The greater part of the gall tissue is composed of elongated, thick-walled cells, the walls of which are much pitted. Here and there little intercellular spaces have remained free. Elongated sclereids, with a distinctly radial orientation, are found in the galls of Cynips kollari C. tinctoria and many others. Occasionally palisade sclerenchyma is produced forthwith in young galls by sclerosis of the assimilatory palisade cells, or the cells of the latter become enlarged before they have hardened to gall-parenchyma. The oak gall of Cecidomyia Cerris (figure 104) may serve as an example of this case.

Even when the cells of the mesophyll divide abundantly, their derivatives often retain the form of typical palisade cells (for instance, in the gall of Cecidomyia tiliacea). If they have hardened near the gall-chamber into a "couche protectrice", we find it composed of palisade cells all oriented parallel to one another. In galls having a different process of development, the sclereids in the vicinity of the larvae cavity are oriented distinctly radially. (The kollari gall and others).

It is interesting that in galls, developing more than one independent zone of mechanical tissue, such as those of Cecidomyia Cerris and very many others, the two mechanical coats are composed of sclereids differing in form. The outer coat consists usually of large cells often elongated like palisade cells, the inner one of appreciable smaller, iso-diametric elements (compare figure 104). We will have to refer later to similar differences.

(240) The differences in porosity of the sclereids is often very striking. In many galls the membrames of the stone cells seem equally closely dotted, the pits standing close to one another (compare, for instance, the cynipides galls shown in figures 107 and 114). In other cases the pitting is relatively scanty, as, for instance, in the oft-mentioned beech gall of Hormomyia fagi,- in numerous galls the pitting of the mechanical cells is completely lacking, at least in many layers. No pitting may be recognized in the upper angular part of the mechanical tissue, in the interesting (Diptera) gall of Parinarium (Fig. 90);- the cells of the lower, flatly arched part and the stone cells which lie on the under surface of the lead (shaded in the figure) are especially porous. Numerous examples might be cited to prove that the mechanical tissues, which surround the larval chambers, are composed of cells with varying porosity and arranged in zones. The side toward the larvae cavity (figure 105N) is often provided with delicate sclereids, in which the thickened ridges resemble slender bands, while in (105R) much thicker cell
(241) walls are met with at some distance from the cavity. These differences may be noticed very clearly, for example, in the gall of Diastrophus Potentillae. In the fagus-gall (figure 103) the delicate cells of the innermost tissue have pitted walls of a kind similar to that known in the thallus of the Marchantiaceae. In the illustration this meshed, most delicate wall-thickening has been indicated in only a few cells. If an outer and an inner mechanical coat may be distinguished, the cells of the first are often only weakly pitted, those of the latter very abundantly so.

Finally those stone cells must be mentioned, which undergo only a onesided thickening of the walls, thus remaining half thin-walled, or in which the wall-thickening in different parts is noticeably unequally strong. One-sided or "horse-shoe" thickened cells occur under normal conditions, for example, in the mechanical ring of the Laurineae;- so far as I know, they are completely lacking in the mechanical tissue of the Cupuliferae. Likewise in oak-galls, we find extraordinarily often that all the mechanical cells, or at least the cells of definite zones and layers, are thickened on only one side. In this way the delicately walled part of the stone cells in many galls comes to lie toward the outside (Apdricus quadrilineatus, Dryophanta folii, Dr. divisa, Neuroterus pallians and many others, compare figures 107 and 114), or toward the center (as in the elliptical gall of the oak, in that of Acraspis macropterae and many others, compare fig. 106). It seems rarely to happen that the cells, thickened on one side, differ also in size and form from the adjacent ones which have become thickened all around (as in the oak gall shown in figure 107). In all cases in which "horse shoe" sclereids occur near others thickened on all sides, they form, as it were, a transition to the delicately walled tissue zones. They
(242) lie either on the inner edge of the mechanical coat (figures

106 and 107), or on both this and the outer edge, furnishing both the transition and the soft parenchyma (Fig. 114). On the other hand, galls are found, in which stone cells, thickened strongly on all sides, directly follow the delicately walled parenchyma. Figure 119 shows finally that even completely isolated zones of sclereids, thickened on half their sides. may occur. It is a matter of course, that this thickening of only half the sides does not exclude the formation of pits. In the gall of Cynips lignicola and many others, the thickened part of the wall is very strongly pitted. We will have to report later on the remarkable phenomena of secondary growth, which has been verified in many of the sclereids of Cynipides galls, the walls of which have been thickened on one side.

Unequally thickened sclereidss, the lumina of which show bottle-neck, pointed forms occur in various Cynipides galls. Compare fig. 107, also fig. 114).

The cells in the gall products of other insects (Stefaniella Trinacriae on Atriplex and others), which are thickened unequally or on half their sides, are rarer and less striking than those of the Cynipides oak galls.

243) 11. Having discussed the qualities of the individual mechanical cells, it will be necessary to investigate the way in which single cells are united into mechanical tissues and what may be the distribution of the mechanical tissues inside the gall body.

In most cases the mechanical cells of galls combine into a close mechanical tissue. Not infrequently, however, a soft parenchyma may be found within this in which isolated stone cells are scattered (compare figure 101). The manner in which the single, thick-walled cells join on to one another, displays nothing unusual; either parallel rows are produced (as in figures 90 and 93) or irregular bands. Small intercellular spaces between the simple sclereids are very clearly recognizable. In order to be able to describe the arrangement of mechanical tissues in the gall body, reference must be made to the other tissue forms in galls.

Lacaze-Duthiers (loc. cit. p. 292), on the basis of his observations on highly organized galls, such as those of Cynips tinctoria and others, differentiated the following tissue layers:

I. (1. epiderme
(2. tissue cellulaire sous-epidermique
(3. parenchyme (spongieuse
((dure
(4. vaisseaux

II. (5. couche protectrice
(6. partie alimentaire

Beyerinck (loc. cit. p. 39) called the two last named tissue forms (II) "the inner gall", the others (I) all together "the gall bark".

The different formation of the couche protectrice, in contrast to gall bark, makes possible the differentiation of the following three types in mechanical gall tissues.

I. The mechanical tissues lie comparatively deep in the inner part of the gall. An epidermis and a bark formed of thin-walled parenchyma is present which can differ greatly in thickness and histolggy.

As an example may be named the gall of Aulex Hieracii: internally each larval chamber is found to be surrounded by a hard protecting layer while a richly developed gall bark lies outside of all. In other galls, the proportion between the gall bark and the "inner gall" varies. In the products of Hormomyia capreae, for example, which exists on willows, only a vewy few layers of bark tissue lie between the mechanical tissue and theepidermis.

2. In forms of the second type, the mechanical tissues lie directly beneath the epidermis. The "gall bark", in Beverinok's sense of the word, is here reduced to the epidermis. The oft-mentioned, undetermined Banisteria gall (fig. 93) bears on its upper side a two layered gall bark, composed of one lgyer of epidermis and a layer of palisade tissue. On the underside, the mechanical tissue lies directly against the epidermis. Figure 90 illustrates similar conditions: merely one layer of epidermis lies above the mechanical tissue zone. Further exam-
(244) ples are furnished by the leaf-curling gall of the Pistaciae, produced by Pamphigus pallidus, P. retroflexus and P. semilunularius. The gall of Andricus coriaceus, abounding on various southern European oaks, consists, at any rate at the time of ripening, only of epidermis and the "inner gall". The mechanical tissues are strongly developed. In the Kollari-gall (produced by Cynips Kollari) the epidermis is thrown off prematurely, so that the outermost tissue layers of the ripened gall are the mechanical ones. (Beverinck loc. cit. p. 150); I found similar conditions in the gall of Cynips Mayri and Küstenmacher (loc. cit. p. 181) in that of C. ferruginea.

3. The third type is characterized by the fact that the mechanical tissues extend to the outer surface of the gall. Even the outermost tissue layer, like those next following, is formed as a mechanical one:- an especial epidermal layer or a "gall bark" can scarcely be spoken of as in Hormomyia fagi (fig. 103), Dryophanta divisa, etc. The outermost layers of the mechanical tissue often consist of cells elongated tangentially, those lying deeper of radially oriented ones. In the ask gall of Diplosis botularia, the cells of the epidermis take part in the sclerosis, at least in places (fig. 110). In this, as in the fagus gall, "enclosed" galls occur of which the epidermis is derived developmentally from the normal one.

The form of the mechanical tissues, corresponds entirely to its significance for the inhabitants of the galls. Speaking teleologically, the question is one of preventing the collapse of the cavity inhabited by the gall animals, of insuring its form and of closing the way into the interior to animal enemies. Accordingly, the mechanical gall tissue usually represents an armor, closed on all sides, which in thickness and extent corresponds more or less to all demands. The question, therefore, whether the firm "mechanical mantel" is only a few cell layers thick or whether practically the whole gall consists of mechanically effective tissues is of no importance for its formal character.

The form of the mechanical mantel usually repeats in miniature the form of the whole gall. In spherical galls, we again find the ball form in the mechanical mantel (figure 108A), in the flat, elliptical oak-gall (B), of the Banisteria gall (E) of the short-cylindrical gall of Parinarium (figure 90) etc., the form of mechanical mantel always follows that of the whole gall. The same conditions are present in sac and walled galls. These do not represent a closed body since an open canal unites the larval cavity with the outer world. A mechanical mantel is also produced here round about the whole. (Fig. 108F). In the leaf-curling gall of Pemphigus pallidus and in others, the up-curled edge of the leaf is pressed so firmly against the lamina, that the shaft for exit scarcely comes under considera- tion in the action of the mechanical tissue developed in the leaf tissue (Fig. 108G). As an exception to the rule, the gall of Cecidomyia tiliaceae (Fig. 108C) should be named. While the gall itself resembles a bi-convex lense, its mechanical mantel has the form of a spindle or a helmet; its long axis being perpendicular to the medial plane of the gall.

The cases deserve special mention, in which the mechanical mantel is composed of two parts. Instead of a hollow ball, it
(245) here resembles two hollow hemispheres with overlapping edges or with edges almost touching each other. The gall of Diplosis globuli, not rare on aspen leaves, opens on the underside by means of a narrow cleft. The lower part of the mechanical man- tel (Fig. 108H) begins immediately at the cleft and, like a bowl set upright, encloses the under half of the larval chamber. The second half of the mantel lies somewhat bent over this;- and, like a hemisphere, protects the upper part of the gall cavity. Between these two parts of the mechanical tissue, lies a thin-walled parenchyma. The galls reproduced in figures 90
(246) and 111 show very similar conditions; in them the upper part of the mechanical tissue has assumed the form of a flat lid.

Usually each gall possesses only one mechanical mantel: a further advance is shown where a second one surrounds the first. While the inner mantel is usually closed on all sides, the outer one is often only half formed;- it then lies like a flat pan over the inner one and over the central gall cavity. (Figs. 104 and 108D). The structure of the ash gall of Diplosis bot- ularia (fig. 108I) is especially firm. On the complete inner mechanical mantel is laid an outer one which is open only on top, showing in cross-section a horse-shoe form. Often both parts, lying opposite the gall opening, unite with one another. In other cases, the outer mantel also forms a closed whole, as, for instance, in the Banisteria gall (fig. 108E), or in that of Cynips Mayri (Fig. 109). In the latter we see clearly that the outer mechanical mantel repeats well the form of the whole gall, while the inner one assumes a simpler spherical form.

If two mechanical tissue mantels are formed in the same gall, the two may almost always be distinguished more or less from each other by their histology.

A very peculiar kind of Cynipides gall is represented by Synophrus politus. On branches of Quercus Super, etc. A small inner cavity encloses the larva. Its anatomical structure is very striking. The protective tissue of the galls if formed of a thick woody-mantel which represents a xylem kernel surrounded by bark, but apparently completely isolated from it, similar to the tuber gnarls spoken of above. The galls also correspond histologically to these. We find in abnormal wood, composed predominantly of pitted parenchyma, that there are places with normally arranged elements lying side by side with others whose fibres, in the greatest "disorder" take first one direction, than an- other. Also the beginnings of "gnarl formations" with strangely bent libriform fibres are not lacking. We often find large sclereids with large lumina and strongly thick- ened walls in the immediate vicinity of the larval chambers. Unfortunately in the dried material I investigated the for- mation of the nutritive layer was no longer recognizable.

If a well differentiated nutritive parenchyma follows, on the inside, the irregular wood layers, the structure must be considered to be a prosoplasma; the gall of Synophrus politus would thus be the only prosoplasmatic one with layers of libriform fibres. However, it shows essentially the greatest correspondence to kataplasmas and we
247) may term it a knarl ball produced by gall animals. The developmental history of this gall, which is not of rare occurrence in Sicily, could not be studied in the specimens at my disposal. A closer investigation of the remarkable structure would be very desirable.

In many galls the "tendency" to form thick walled parenchyma cells is very great and is not thoroughly exhausted in the production of the mechanical mantels just described. Galls which contain sufficient quantities of thin-walled bark parenchyma in young and medial stages of development finally consist only of sclereids - at times after the disappearance of the tender nutritive tissue. An example of this is the large gall of Cynips Mayri, in which the luxuriant tissue masses between the outer and inner mechanical mantels finally become entirely thick-walled and lignified (fig. 109).

As in the consideration of normal parts of plants, it is also not admissable to consider here all thick-walled cells as mechanically acting parts which function expediently. Besides, the sclereid tissue, produced late in many galls, is often so porously constructed that there can be no thought of a mechanically effective tissue.

(248) Nevertheless, besides the above named sclerotic tissues, we find still others which function very obviously as such and deserve brief mention.

I would name first of all the closing tissues. I thus term those tissues which are used to assist in tightly closing the entrance of the gall, because of their suitable cell forms. In many walled galls, short, extraordinarily thick-walled papillae are produced on both sides of the entrance to the gall cavity, and form a cogging of the two contact surfaces. Figure 110 shows part of a cross-section through the gall of Diplosis botularia. The papillae are short and rounded, apparently acting similarly to the same structures of the cone-scales in conifers[1]. Since these peculiar hair structures in the botularia gall are formed only on the surfaces touching one another and in their immediate vicinity, it might be well to make investigations as to whether locally acting stimuli (perhaps stimuli of contact?) possibly cause their formation[2].

Further, the mechanisms of opening deserve our attention. Many gall animals free themselves from their enclosures by eating their way out of their dwelling place. In others, the host plant produces the necessary mechanisms which, at the time of ripening, give the gall animals their freedom. The mechanism is set in action as soon as the tissues of the gall begin to

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[1] Tubeuf. Haarbildungen d. Koniferen. Forstl.- Naturwiss. Zeitschr., 1896. Bd. V, p. 109. Compare plate VI, fig. 3.

[2] It might be possible that here, as well as in other gall formations, the chemical stimulus, arising from the gall poison, participates only indirectly in the production of definite forms, since it only makes the tissues susceptible to other kinds of stimuli.

shrink,- the unequal water content of the mechanical tissues and the soft parenchyma causes an unequally strong contraction; thereby bringing about a rupturing of the gall tissue. The undeterminable (Diptera?) gall of an Anherstiee[1] is very strikingly constructed. A cross-section through the gall shows (fig. III) that the mechanical mantel consists of two isolated
(249) parts. A flat, cover-like plate of tissue lies above the larval chamber, the edges of which extend over and around the flatly curved, bowl-like sclereid mantel lying beneath the cavity. Between the two are a few layers of delicate tissue. When the gall dries, this tissue degenerates and the cover falls off in one piece, thus opening the interior of the gall. The mechanical tissue of the gall illustrated in figure 90 may indeed function very similarly, but my dried material did not permit of any conclusion concerning this. Our native flora furnishes further examples. At the base of the gall of Hormomyia fagi (compare fig. 86) a delicately walled zone of separation is retained, - so that at the time of ripening, the helmet-like part of the gall lying above this zone is loosened. In the linden gall of Cecidomyia tiliacea the sclerosized inner part of the gall, which contains the larval cavity, is squeezed out of the contracting peripheral tissue and the inner gall falls to the ground. Later, as described by Kerner[2], the gall animal gnaws a regular groove in the gall kernel and then pushes off the upper part, like a cover. Figure 112 illustrates this process. Further examples are described in Kerner's "Pflanzenleben".

Nutritive Tissues

Those gall tissues which are devoured by their inhabitants, or the contents of which at least are of benefit to them, may be termed nutritive tissues. The form of the single cells and the character of their walls are of less interest to us here than is their distribution inside the gall body and the quality of their contents.

The significance of the nutritive tissue in the histology of the gall formation and for the existence and development of the gall animals even exceeds that of the protective tissues. No gall is without nutritive tissues and these not infrequently represent the chief mass of the gall body. In the discussion of gall hypertrophies and kataplasmas, we have already become acquainted with galls in which all the pathological cell products, without an exception, bear the character of nutritive
(250) cells. It is usually a question of the deposition of proteins, of oil and of starch,- as stated above in the discussion of Erineum hairs. The fact is here of interest, that, in prosoplasmas, the "division of labor" among gall tissues produces definite zones, the cells of which "serve" exclusively for the storage of carbo-hydrates or of food stuffs containing nitrogen. Especially in the highly organized cynipides and diptera galls, the layers of the nutritive tissue are extraordinarily sharply set off from the neighboring, mostly sclerosized zones. Lacaze-Duthiers, in his gall anatomy, differentiated an especial "couche alimentaire" (see above).

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[1] According to Professor Radlkofer's kind determination. For the shipment of material, I wish to thank Mr. Zenker in Bipindi.

[2] Pflanzenleben, 1898, Bd. II, p. 484.

In a "normal" development, the contents of these nutritive sues are devoured by the gall animals. Under abnormal conions, however, the nutritive material of the plant cells themselves may be used. Galls of Pediaspis Aceris (cynipides), freed from their inhabitants and left in solutions which are poor in food stuffs, or in ordinary tap water, remain alive for weeks; but the contents of the nutritive tissues disappear. If galls of a similar kind, ceteris paribus, are put in a sugar solution, the contents of the nutritive tissues remain unused or may even be slightly increased.

We will distinguish two forms of nutritive tissues: the nutritive epidermis and the nutritive parenchyma. Nutritive tissues of the first kind are present, when, for example, in sac galls or walled galls, the space occupied by the gall animals is lined with a clearly recognizable epidermis, which functions as nutritive tissue. Very often, delicate walled hairs, which are extraordinarily rich in food stuffs, are produced on it which we will term nutritive hairs. We speak of nutritive parenchyma, when the well-filled cells belong to the ground tissue. This form of nutritive tissue plays a large part especially in medullary galls. The nutritive parenchyma usually consists of many cell layers, which can differ greatly among themselves, in the quality of their contents. A double "nutritive mantel" may be often developed, just as in many galls the larval cavities are protected by a double mechanical mantel. The inner nutritive zone is then enclosed by the mechanical tissue and belongs to the inner gall; the other lies outside the mechanical mantel and belongs therefore to the gall bark. Conditions are very complicated, when two mechanical and two nutritive mantels are present.

Nutritive Epidermis

We find a nutritive epidermis in many leaf sac galls, which have been produced by Phytoptes and Aphides. The inner epidermis of the infected part of the leaf remains delicate, develops only a thin cuticle and is usually richly filled with albuminous stuffs. There is nothing unusual about the form of the cells, so long as they do not grow out into hairs - nutritive hairs.

We find papillae-like structures in the larval chamber of the gall of Cecidomyia Ulmariae; the cells are strongly curved outward, their menbranes being often considerably thickened. Nutritive hairs occur on the inner side of different mite galls and in their simple form seem similar to certain Erineum hairs in size as well as amount of cell contents (compare figures 85a and 113a). Albuminous substances abound in their lumina, such as drops of fat and also small grains of starch. Small papillae
(251) or flask-like hairs are found on the galls of many Aphides (on Populus Pemphigus spirothece)[1] on Ulmus Tetraneura compressa (figure 113B) and many others.

Nutritive Parenchyma

It is evident that no sharp line may be drawn between the superficial nutritive tissues, which still bear distinctly the character of the epidermis, and the inner ground tissue complexes of the nutritive parenchyma, since many walled galls, which, as we have seen, are lined with epidermis, can grow into completely closed balls etc., the cells of the epidermis then often undergoing the same development as the cells of the bordering ground tissue layers.

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The distribution of the nutritive parenchyma in galls is into various types. In the simplest and most frequent case, an inner nutritive mantel is formed only within the mechanical tissue, is at once accessible for the occupants of the gall, and is usually unsparingly devoured by them. In more complicated cases, abundant quantities of food stuffs are deposited outside the mechanical mantel. The cells of this outer mantel, however, are not consumed by the gall animals, but rather their contents become accessible for the larvae only by breaking through the sclereid layer.

(252) The form of the simple nutritive cells shows little variation. Usually iso-diametric elements are concerned here, elongated, for example, into sac-like forms in the elliptical galls of Neuroterus lenticularis. I found very delicate, elongated cell threads, comparable to branched algae, in the outer nutritive mantel of an undetermined Cynipides gall of Quercus Wisliseni (figure 114 St). While the nutritive tissues in general usually consist of a dense parenchyma, wide intercellular spaces remain free in the outer nutritive mantel of this gall. The form of the nutritive tissues, as a whole, is connected in general with that of the mechanical mental, or of the entire gall.

In regard to the cell contents, two different zones of nutritive tissue usually come under consideration in highly organized Cynipides galls.

The cells of the innermost layers, on which the larvae feed, contain regularly a cloudy, dense cytoplasma, in which numerous small drops of fat are often mixed. We term this innermost layer the protein layer. Figure 115 shows a cross-section through the maple leaf gall of Pediaspis Aceris; all the cells are thin walled, the outermost being rather small, the innermost strikingly large. The cells bordering directly on the larval cavity are filled with a cloudy mixture of cytoplasma and fatty oil. There are here and there a few clear vacuoles in the emulsion.
(253) In most galls, several layers are found, the cells of which are filled in the same way with proteins etc. If a mechanical mantel is also developed, the nutritive tissue lies, of course, inside the sclereid tissue.

Starch also should come under consideration. In any kind of galls - in many kataplasmas and in many Erineum galls - starch is usually present in abundance and always lies outside the protein layer. We term it briefly the starch layer. Either both the protein and starch layers belong to the inner gall, lying therefore inside the sclereid tissue, or the starch tissue is deposited partially or entirely in the gall bark. The elliptical galls of our native oaks (Neuroterus lenticularis etc.) store up the greater part of their larval food outside the mechanical mantel,- at times, almost the entire gall bark represents a gigantic reservoir of food stuffs. An especially complicated case is that illustrated in figure 114; the starch layer (St) lies about the inner mechanical mantel and on it a second mechanical mantel.

It should be noted that the contents of the nutritive cells, which contain starch, are dissolved before being used, and, according to Beyerinck's investigations, are converted into proteins and fats.

In the nutritive tissue of many galls two striking bodies are found, in the cell contents, which Hartwich[1] has thoroughly investigated. Besides balls of "tannic substances", to which I will return later in brief, cysto-ligh-like forms are also found, which give the reaction of wood and which we, with Hartwich, will term lignin bodies. According to Hartwich, they are produced at the corners, where several cells come together, as local thickenings of the walls (fig, 116a) swelling up to sphero-crystalline tubers and finally taking into requisition the entire cell (fig, 116b). Also, in later developmental stages, the concentric arrangement of their layers is often very distinct. They color red with phloro-glucin and hydrochloric acid - not all the layers equally quickly nor equally intensively.

(254) It is still uncertain whether the lignin bodies are of any special significance for the occupants of the galls. Doubtless they are consumed by the larvae, bug it seems improbable that they contain nutritive material[2]. They have been found as yet only in a limited number of galls, in fact only in the Cynipides galls of various species of Quercus. Hartwich mentions them in the galls of Cynips tinctoria, (on Quercus infectoria) of Cynips lignicola and in an undetermined Texan gall on Qu. virens. Further, I found the same structures in the galls of Cynips strobliana and Chilaspis nitida (the latter on Qu. Cerris). The cells provided with lignin bodies either form a continuous layer in the nutritive tissue of the galls (as in the galls of C. tinctoria etc.) or may be found in groups here and there outside the mechanical mantel, in the gall bark (ripe galls of Chilaspis nitida).

Although the cells of the nutritive tissue are gnawed by by the gall animals, secondary phenomena of growth may at times be enacted in them. Either hypertrophic or hyperplastic changes may occur in them. Beverinck (loc. cit. p. 84, 113) has determined in the elliptical gall of the oak that the sclereids thickened on one side, which were mentioned above, may supplementarily grow out to resemble tyloses, while the part of the epidermis which has remained delicate, undergoes a strong superficial growth, thereby causing the production of a secondary nutritive tissue.

In other cases the cell material, upon which the gall animals feed is replaced by a new outgrowth, resembling callus, as in the gall of Nematus Vallisnerii - which Frank[3] investigated developmentally,- and still others.

Besides those tissues which protect and nourish the occupants of the gall, all others in the galls play a very subordinate part. We may content ourselves with a brief description of them.

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[1] Ueb. Gerbstoffkugeln u. Ligninkörper in d. Nahrungsschicht der Infectoria-Galle. Ber.d.D.Bot. Ges.,1885, Bd. III, p. 146.

[2] Recent investigations have made improbable my earlier expressed point of view (Beitr. z. Anat. etc. lot. cit.) that the lignin bodies like the carbo-hydrates and proteids of the nutritive parenchyma furnish food stuffs for the gall-insects.

[3] Krankh. d. Pfl., 2. Aufl., Bd. III, p. 201.

3. Assimilatory Tissue

One characteristic of almost all galls is their poverty in chlorophyll. Very many prosoplasmas to be sure are a pale green such as the half-transparent products of Spathegaster baccarum, Hormomyia fagi, etc., but their chloroplasts are scanty, small, twisted and only weakly colored. In very many, such as the various elliptical galls, the Terminalis, Folii, etc. no chlorophyll at all may be found under the microscope at the time of ripening.

The gall of Nematus Vallisnerii (on Salix), for example, should be considered an exception to the rule. When a gall of this kind is broken open, the extensive deep green tissue complex inside it is strikingly noticeable even macroscopically. The outermost layers consist either of elements elongated into
(255) a palisade form, or roundish ones as clear as water. Then, towards the inside, comes a thickly developed, assimilatory parenchyma (compare also figure 88), which is far stronger than the normal mesophyll of the willow leaves.

The large galls of Aulex Glechomae, rich in water, which deform leaves and stalks, develop superficially an assimilatory tissue which is pale green in color and consists of one or more palisade layers.

In the sac galls, which Phytoptus macrorrhynchus usually produces very abundantly on the leaves of Acer Pseudo-platanus, a large-celled, colorless parenchyma or one containing anthocyanin, is formed on the outer side (the morphological upper side of the leaf) and on the inner side (the morphological under side) a cell layer which, pale green in color, resembles a palisade tissue (fig. 117).

Cases are not really rate in which the galls carry over unchanged the assimilatory tissue of the organs which bear them, (many stalk and leaf galls; compare, for example, figure 93). Since products of pathological tissues are not concerned in these, we may pass them by.

4. Vascular Tissues

The relation of the galls to the vascular bundles of the plants which bear them is unmistakable. Many are produced directly from the tissue of the vascular bundles, others are connected throughout with the neighboring vascular tracts. The vascular bundles are usually very sparsely formed, and only as delicate cords, inside the galls themselves,- in kataplasmas, as in prosoplasmas.

The individual elements of the vascular bundles resemble normal ones; yet the individual ducts usually have very narrow lumina. Tracheids abound and, for their part, often repeat the form of the parenchyma cells. In many galls,- for example, in that of Spathegaster baccarum,- the composition of the vascular bundles and the form of the separate tracheal elements resemble throughout the corresponding cells of many callus tissues. (Compare fig. 67).

(256) The structure of the vascular bundles likewise in general is similar to the normal one. The galls of Andricus albopunctatus and Trigonaspis megaptera should be named as exceptions, which, according to Beverinck (loc. cit. p. 128) have concentric

bundles[1]. The arrangement of the bundles in the gall body varies greatly. They are either placed in a circle, as in the normal axillary parts of dicotyledons, thus turning the xylem toward the larval cavity, the phloem toward the outerside of the gall, (reversed according to Beverinck, in the gall of Aphilothrix Malpighi), or they pass through the bark of the gall as a delicate net work as may be found in the fleshy pericarp of many fruits. Courchet[2] has explained the double vascular bundle ring in the gall of Pemphigus cornicularis by peculiar processes of folding and coalescence in the organ bearing the gall.

5. Aerating Tissues

In general, the tissues of the galls are even more porously constructed than are the likewise mostly porous callus tissues. Almost everywhere at least small intercellular spaces are distinctly recognizable, so that provision of air is assured for the gall tissues and gall occupants. The porous texture of the bark tissue in many Cynipides galls is very striking. The single cells are provided with long slender arms, by which they are connected with one another;- between the single cells lie extensive
(257) intercellular spaces. Figure 118 gives a few cells of this kind of star-parenchyma from the Kollari gall. In other cases, instead of star-like cells, elements distended into pouches are formed which are connected with one another only at their slender ends, or through especially short pointed protuberances. We find the same conditions in the tissue of bark excrescences and lenticel outgrowths;- of the native Diptera galls, that of Diplosis tiliarum, for example, is especially rich in "aerating tissue" of the kind described.

In the Kollari gall, the Argentea gall etc., the star-like parenchyma cells lignify in the later developmental stages and take on an abundant pitting. In the gall of Cynips Mayri, cells of no inconsiderable wall thickness are produced.

The question must remain open as to whether the air-reservoirs, furnished in these tissues which abound in interstices, can in any way aid the well-being of the gall animals and in so far be termed "expediently" functioning tissue forms. As already indicated, very similar tissue and cell forms also occur in other kinds of pathological products (for example, bark excrescences), in which from the very beginning the question as to any "purposefulness" is known to be unfounded.

Tissues which contain air occur also in other galls. The characteristic white markings of the gall of Andricus quadrilineatus are produced by flatly raised ridges, which consist of tissue abounding in interstices. The gall of Aulex Hieracii is traversed meridionally by tissue stripes which contain air.

Pneumathodes occur in galls in the form of stomata and lenticels. In the "enclosed" galls, the stomata of the normal epidermis are always changed in so far that they often lose their ability to close, remaining open permanently;- for example, in many Nematus galls. In the galls of Dryophanta folii, Dr. divisa, Dr. longiventris, etc., Kustenmacher found that the guard cells

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[1] Vascular bundles with abnormal arrangement of the phloem occur also in correlation-heteroplasmas (p. 252).

[2] Etude s. l. galles prod. par les aphidiens. Montpeilier, 1879.

which touch one another at their tips, become pitted on the contact walls, "the walls are reabsorbed, the two guard cells thus appearing later as ring cells, which serve less in closing the air passage, but rather stiffen it". In general the galls do not abound in stomata. I know of no case as yet, in which, then the epidermis makes an active surface growth, the number of the stomata is increased in correspondance with the increase in surface. The tissue lying directly under the stomata often abounds in interstices and forms, at times, a small cushion on the top of which lies the stoma.

Lenticels are especially noticeable on the various Nematus galls of the willow. The stomata, together with the adjacent parts of the epidermis, soon disintegrate and large, roundish lenticels develop beneath them, which as brown dots, often give the galls a very characteristic appearance. The lenticels on the galls of Nematus gallarum on Salix grandiflora are especially large and numerous. In Nematus bellus one or two especially large lenticels are present on that part of the gall which belongs to the upperside of the leaf. In moist air, lenticels develop the excrescences already described just like those of the normal parts. Aphis galls also are at times rich in lenticels,
(258) especially those of Pemphigus spirothece and P. bursarius. Not only the galls themselves, but even the adjacent parts of the petioles and the midrib swell greatly at times and develop numerous lenticels.

Küstenmacher has found holes in the epidermis of various galls which he terms carbondioxid fissures. The carbon dioxid fissures are simply epidermal cells, which are separated from one another and between which the intercellular space is open to the outer air. They usually have small lumina and lie at points, where several cells touch at the corners. The upper opening is usually three-cornered".

"I have named them carbon dioxid fissures, because I think they have been produced by an inner pressure in an intercellular space too far distant from other air passages, which pressure is caused by the freeing of carbon dioxid (loc. cit. p. 181)".

According to Küstenmacher, under certain circumstances, pores in the membrane can also discharge the functions of pneumathodes.

"The sieve hairs of the Cecidomyia gall, the normal fascicular hair of Hieracium and the hairs of the Ferruginea gall, are, according to Küstenmacher,- "organs which can convey air into the interior of the cells".

In these statements, of course, it is only a question of hypotheses, and, as I believe, very improbable ones.

6. Secretions and Secretion Reservoirs

The secreting elements of the normal epidermis and those conveying the secretions, are either found again in gall tissues in an unchanged form, or a rich increase of the elements furnishing the secretions takes place. According to Küstenmacher, in the formation of the Cecidomyia galls on Artemisia campestris, the oil pores of normal plants act absolutely passively. Among the galls of Eucalyptus, of which I investigated herbarium material, forms may be found which are practically free from secretory pores, side by side with those whose parenchyma is penetrated throughout by them[1]. In many other galls also, as in the formation of wound-wood and gall wood, the increase of the intercellular spaces containing secretions plays an important part;- as for example, in many Pistacia galls (such as that of Pemphigus semilunularius and many others).

Less frequently, new forms of secreting cells and tissues occur in galls, which are not known in the anatomy of the normally developed host plants. I include among these a peculiar gland, which I found in the interior of a Cynipides galls (on Quercus Wislizeni). This galls may be illustrated here as an example of a richly differentiated form (fig. 119). The secreting superficial cells are still to be mentioned;- such as occur, for instance, in the gall produced by Cynips argentea
(259) on Quercus pubescens[2], in that of Andricus Sieboldii, in the Bassorah galls[3] etc. The galls of Cynips Mayri appear similarly "varnished". Unfortunately I could no longer recognize the structure of the secreting cells in the dry material at my disposal[4].

Crystals of calcium oxalate are not generally found in abundance in galls,- and we could verify the same scarcity in many callus tissues. The entire absence of crystals seems to be rare. Vandevelde[5] has published some statements on the scanty crystal content of those plant organs, which have galls.- Likewise, cases are not lacking, in which, we may find a rich crystal formation in the galls. Kohl has emphasized the fact, that forms rich in sclereids often contain crystals[6]. In others the crys-
(260) tals occur as an accompaniment of the fibro-vascular cords. Cells bearing crystals and united in radial rows are found in Tinctoria galls and in others. In the products of Cynips Hedwigii and Dryophanta verrucosa, certain layers of the gall tissue are especially rich in crystals (according to Küstenmacher). I found in the fagus gall (fig. 103) that all the cells which bear crystals and are at an equal distance from the surface of the gall had been united into a special layer, which lay on the boundary line between the large-celled outer tissue and the small-celled inner one. The cells are often divided by exceedingly delicate cross-walls; each division containing a single crystal. In numerous galls we find that continuous layers of crystal cells arise through the abundant but localized production of crystals, these cells layers, in many forms, lying in the gall bark; in others, in the inner gall.

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[1] The diversity of Eucalyptus galls is surprisingly great. The tests, which I had opportunity to investigate, lead me to expect many an interesting result from a comprehensive treatment of Eucalyptus galls from a developmental and histological standpoint.

[2] Compare Hieronymus. Gallen aus Südamerike und Italien. Ztschr. f. Entomol., 1892. Bd. XVII.

[3] Hartwich. Arch. d. Pharm., 1883, p. 829.

[4] Investigations on fresh material would be very desirable - the gall is abundant in Sicily.

[5] Bijdr. tot de phys. der gallen, het aschgehalte d. aangetocte bladeren. Bot. Jaarb. Dodonea, 1896, Vol. VIII, p. 102.

[6] Anatom.- physiol. Untersuch. d. Kalksalze etc. Marburg, 1889.

Finally the content in tannic substances should be considered, which, as is well known, makes many galls of practical importance. Those galls are histologically interesting in which the storage of the tannic substance is restricted to definite zones. The bark of many Cynipides galls is strikingly rich in this. In them the tissue, resembling star-parenchyma since it abounds in interstices, is filled with the substances. The antiseptic action of the tannic substance may, under certain circumstances, be of significance in the development of the galls and their occupants. Nevertheless, it is noticeable, that, "tannic substance balls"[1] may be found in the nutritive parenchyma of many Cynipides larbae, and are devoured by the gall animals, but are, according to Hartwich, thrown off again as excreta. According to Beverinck (loc. cit) and Hartwich, forms which are at once conspicuous because of their very dark color, occur in the various elliptical galls, in the products of *Cynips Kollari*, *C. lignicola*, *C. insana* ("Bassorah galls"), *C/ tinctoria* etc. Also they are known already to Lacaze-Duthiers. For the tannic substance in other hyperplasias, compare p. 167.

Finally, the anthocyanin content of many galls should be mentioned. Many galls, just like normal fruits, get "red cheeks" through the action of light (*Nematus gallarum*, *Hormomyia fagi*, etc.); a reddish tone is thoroughly characteristic of many (*Cynips terminalis*, very many Phytoptus sac galls etc.). In many others the anthocyanin content is restricted to definite parts of the tissue. The red zones, ten or more layers thick, in the galls of *Nematus Vallisnerii* (on Salix) are very noticeable. On the upper side (the side toward the light) the cell layers derived from the mesophyll become colored unusually highly - those derived from the epidermis were colorless in the examples which I investigated.

The present pages give indeed no exhaustive anatomy of prosoplasmatic galls;- only the outlines of such an one - corresponding to the task of our book - may be given here. What is
(261) responding to the task of our book - may be given here. What is given may well furnish sufficient material for a comparison of the various pathological tissue forms with one another,- which we consider the aim of this exposition. New points of view for our question would scarcely have been acquired by a deeper investigation of the galls, which have been studied up to the present.

In conclusion, we should remember that the number of galls which have been closely investigated is still very small; we know practically nothing concerning the forms outside of Europe or in the tropics, least of all concerning their anatomy and development. And also a thorough study of the native galls is in many cases still urgently desired.

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[1] Hartwich, loc. cit.

(262) Our theme is exhausted with the discussion of the various abnormal tissue forms, which led us from simple hypoplasias to highly organized prosoplasmas, since the many forms, furnishing information concerning abnormal cytological structures, and, further, all phenomena of degeneration and all micro-chemical conditions, varying from the normal, must remain excluded from our presentation of this subject.

An active interest in cytology has brought to maturity in the last decade, a quantity of zoological and botanical publications, many of which either consider abnormal structural conditions as well as normal ones, or treat of the former exclusively. Of the zoologists and anatomists, I till name only Arnold, Cornil, Denys, Hansemann, O. Hartwig, Hass, Schottländer and Stroehe[1]. Instead of an exhaustive survey of the botanical literature, I will give below only a small selection,- especially in order to indicate the various questions, with which attempts have been made to approach the problems of "pathological cytology"[2].

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[1] Citations of literature in O. Hartwig, Ueb. patholog. Veränd. d. Kernteilungsprozesses infolge experimenteller Eingriffe. Festschr. f. Virchow, Berlin, 1891, Bd. 1, p. 197. Albrecht, Physik. Fragen der Zellpathologie. Ergebn. d. Allg. Path. u. s. w., 1901, Bd. VI, p. 900, 1902, Bd. VII, p. 783. Ziegler, Allgem. Pathologie. Jena, 1901, p. 300 and places given.

[2] Contributions to the "pathological cytology" of plants were furnished - besides by many others - by Andrews, Wirkung der Centrifugalkraft auf Pfl. Pringsh. Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 1. Blazek, Einfl. von Bensoldampfen auf pflanzliche Zellteilung. Abhandl. böhm. Akad., 1902 Bd. XI, Nr. 17. Buscalioni, Osservaz. ericerche sulla cellula vegetale. Ann. R. Ist. Bot. Roma, 1898, Vol. VII, p. 255. Cavara, Ipertrofie ed anomalie nucleari etc. Riv. Patol. veg., 1896, Vol. V, p. 238. Dangeard et Armand, Observ. de Biol. cellulaire. Le Botaniste, T. V., p. 269. Dangeard, Sur le caryophysems. C. R. Acad. Sc. Paris, 1902, T. CXXXIV, p. 1365 (compare also Mem. s. l. paras. du noyau et du protopl. Le Botaniste, T. IV, p. 199). Gerassimow, Die kernlosen Zellen der Konjugaten. Bull. Soc. Imp. Natur. Moscou, 1892, p. 109. Grant, Multinucleated condition of the veget. cell etc. Transact. Proc. Bot. Soc. Edinburgh, Vol. XVI, pt. 1, p. 38. Heidenhain, Einiges ueber d. sogen. Protoplasmaströmungen. Sitzungsber. Mediz. Phys. Ges. Würzburg, 1897, p. 116. Hottes, Ueb. d. Einfl. von Druckwirkungen auf die Wurzeln von Vicia Faba. Diss. Bonn. 1901. Huie, Changes in the Cell-organs of Drosera rotundif. Quart. J. Micr. Sc. 1897, Vol. XXXIX. (Ann. of Bot., 1897, Vol. XII, p. 560), and 1899, Vol. XLII, p.203. Juel, Kernteil in d. Pollenmutterzellen v. Hemerocallis u. s. f. Pringsheim's Jahrb. f. wiss. Bot., 1897, Bd. XXX, p. 205. Klebs, Beitr. z. Phys. d. Pflanzelle. Tubingen Untersuch., 1888, Bd. II, p. 489. Kohl, Z. Phys. des Zellkernes. Bot. Cbl., 1897, Bd. LXXII, p. 168. Magnus, W., Studien an der endotrophen Mycorrhiza von Neottia

(Footnote 2 continued)
Nidus avis. Pringsheim's Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 205. Massart, Cicatrisation ch. l. vegetaux. Extr. Mem. cour. Acad. de Belge, 1898, T. LVII, p. 37. Natruchot et Molliard, Certains phénom. prés. par l. noyaux sous l'action du froid. C. R. Acad. Sc. Paris, 1900, T. CXXX, p. 788., Modific. de struct. observ. d. l. cell. subissant la fermentation propre. Ibid., p. 1203, Modifications prod. par le gel d. la struct. d. cell véget. Rev. gen de Bot., 1902, T. XIV, p. 401. Molliard, Hypertrophie pathol. d. cell. végét. Rev. gén. Bot., 1897, T. IX, p. 33; S. l. caractères anatomiques de Hémiptèrocéc. foliaires, Mém. déd. au prof. A. Giard, 1899, p. 489. S. qs. caract. histol. d. cecidies prod. par l'Heterodera radicicola. Rev. gen. Bot. 1900, T. XII, p. 157. Miehe, Ueb. Wanderungen d. pflanzl. Zellkernes. Flora, 1901, Bd. LXXXVIII, p. 105. Mottier, Effect of Centrif. force upon the cell. Ann. of Bot., 1899, Vol. XIII, p. 325. Nawaschin, Beob. ueb. d. fein. Bau. u. Umwandl. von Plasmodiophora Brassicae u. s. f. Flora, 1899, Bd. LXXXVI, p. 406. Nemec, Cytol. Unters. an Veget.-punkten d. Pfl. Sitzungsber. Bohm. Ges. Wiss., 1897, Nr. XXXIII, p.489. Ueb. abnormé Kernteil. in der Wurzel-spitze v. Allium Cepa. Ibid., 1898, N. IV. Ueb. Kern- u. Zellteilung bei Solanum tuberosum. Flora, 1899. Bd. LXXXVI, p. 214. Zur Phys. der Kern- u. Zellteilung. Bot. Cbl., 1899, Bd. LXXV, p. 241. Ueb. den Einfluss niedriger Temperaturen u. s. f. Sitzungsber. Böhm. Ges. Wis., 1899, N. XII. Ueb. experim. erzielte Neubildung v. Vakuolen u. s. f. Ibid., 1900, N. V. Die Reizleitung u. d. reizleit. Strukt. bei d. Pfl., Jena, 1901. Paratore, Ricerche istol. sui tubercoli radicali delle Leguminose. Malpighia, 1899, Vol. XIII, p. 211. Prillieux, Alternations prod. d. l. pl. par la culture d. un sol surchaufie. Ann. Sc. Nat. Bot. 1800, serie VI, T. X, p. 347. Rosenberg, Phys.-cytol. Unters. ueb. Drosera rotundifolia, Upsala, 1899. Schrammen, Einwirkungen v. Temperaturen auf die Zellen d. Vegetationspunktes d. Sprosses v. Vicia Faba. Dissertation Bonn. 1902. Schwarz, Fr., Morph. u. chem. Zusammensetzung d. Pl. Cohn's Beitr. zur Biol. d. Pfl., 1887, Bd. V, p. 1. Shibata, Experim. Studien ueb. d. Entwickelung d. Endosperms bei Monotropa. Biol. Cbl. 1902, Bd. XXII, p. 705. Strasburger, Zellbildung u. Zellteilung, 3. Aufl., Jena, 1880. Ueb. Plasmaverbind. planzl. Zellen. Pringsheim's Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 493. Tischler, Ueb. Heterodera-Gallen u. s. f. Ber. d. D. Bot. Ges., 1901, Bd. XIX, p. (95). v. Wasielewski, Theoretische und experimentelle Beitr. z. Kenntnis d. Amitose, Pringsheim's Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 377. Zimmermann, Morph. u. Phys. d. pflanzl. Zellkernes, Jena 1896. - Compare further the critical work by A. Fischer, Fixtierung u. Bau d. Protopl. (Jena 1899), in which is named a number of further works, pertaining to this.

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(263) In abnormal cytological conditions, there usually occur variations of the following kinds:

1. It may be a question of an abnormal arrangement and distribution of the cell elements - as a result of mechanical interference, for example, in the use of centrifugal forces, or after plasmolysis and so forth, or as the especial effects of stimulation, for example, in the migration of the nucleus or the phenomena of currents in the cytoplasm after injury and the like.

2. Or it may be a question of an abnormal form and structure of the cell organs - such as the abnormal form of the dormant nuclei, the abnormal distribution of its chromatin, abnormal figures in cell division, or of amitoses, pseudo-amitoses, abnormal cytoplasm structures and so forth.

3. Or there may exist variations from the normal conditions of size and number - hypertrophies of the nucleus, increase of the cytoplasm, definite kinds of cytoplasm, of vacuoles, nuclei, nucleoli, contraction of the various organs, and so forth.

Besides this, those various processes of degeneration come under consideration, which might be separated only with difficulty from many of the phenomena here described.

(264) If I have given here no detailed treatment of cytological questions, it was because our present knowledge of the normal cytological processes seems to me still too little understood to warrant an all inclusive discussion of the abnormal conditions. I have therefore limited myself to calling attention, here and there in the text, to changes in the nucleus, the figures in the cell divisions and so forth, if the abnormal cytological conditions seemed suited for completing the characterization of any abnormal tissue forms. The short bibliographical-summary given here will perhaps suffice, for the present, for further orientation.

The phenomena of degeneration and necrosis can be considered as physiologically well-characterized sub-divisions of those namdd above.

It is according to whether we take into consideration the parts of cells which disappear during degenerative processes, or those newly produced products of decomposition, that we will be able to distinguish various groups of degenerative phenomena, which I have mentioned only by way of suggestion in the preceding chapters and then only if they helped to characterize the abnormal tissues which interested us.

Of primary interest is the degenerative disappearance of the cytoplasm, of the nucleus and of the chromatophores in starving cells (phenomena of inanition), in the parts of tissues sucked dry by parasites, or in those cells which are incited to abnormal (kataplastic) growth by some stimulus (hyperhydric tissue p. 80, callus hypertrophies p. 93 and many others). The protoplast becomes inpoverished, the nucleus disappears, the chromatophores become paler and smaller apparently changing back into leucoplasts. Many of the cases described above prove that all the living parts of the cell degenerate equally quickly and in the same way; that under conditions, which, for example do not endanger the continued existence of the nucleus, the very sensitive chlorophyll grains can disintegrate and the like; or that the cytoplasm often can outlast the nucleus and the walls of the vacuoles in the former often prove themselves to be the most rësistant parts.

All parts of the plant cell can be changed degeneratively. We can distinguish, according to the products formed, a

slimy and gummy degeneration to which whole cells, including their cellulose covering, may often fall victim (diseases of "liquefaction", gumming and so forth);

degeneration into vacuoles, in which the cytoplasm becomes filled with numerous vacuoles assuming a coarse foamy structure;

fatty degeneration, characterized by the occurrence of oil drops in the cells;-

cellulose degeneration. I believe I have found in those sacs, in which (as the clearage product of decayed cytoplasm) inter-cellular cellulose precipitates are produced, as in the cases studied by W. Magnus (loc. cit) and those described in the third chapter (P. 63).

Besides the products of decay already named, the precipitates, "granula" of an unknown kind, should be mentioned, which are often found in diseased cells. Also, many of the artifacts are included here which owe their production to various fixing media.

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We may perhaps look for the results of a degenerative decay of the cytoplasm in the abnormal processes of suberization or lignification (p. 64)[1].

The abnormal micro-chemical conditions lie outside of our consideration. The conclusions to which micro-chemical facts lead us are connected only very loosely with anatomy, but more closely with chemical physiology. Numerous works[2] have already thrown light on abnormal acidity, on abnormal distribution of tannic substances, of sugar, nitrates, alkaloids, on the production of foreign matters, on the abnormal composition of the cell membrane and the like,- It is not our task to go more into detail as to the contents of these works.

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[1] The literature appertaining to this is not especially abundant. Besides many of the works above named, there may be considered also, Klemm, Desorganizationserscheinungen der Zelle, Pringsheim's Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 627. Sorauer, Handb. d. Pflanzenkrankh., 2. Aufl., 1886, Bd. 1, p. 861 (on "liquefaction diseases"). Frank, Krankheiten d. Pfl., 2. Aufl., 1894, Bd. I. p. 31, 43, 103, etc. (Protection and core-wood secretions on wounds, phenomena of decay). Hartig, R. Zersetzungsverscheinungen des Holzes, Berlin 1878. On the formation of wound-gum, compare also p. 165) note 2. Phenomena of disorganization were observed in living cells, among others by Haberlandt, Kulturversuche m. isolierten Pflanzenzellen. Sitzungsber. Akad. Wiss. Wien, 1902. Bd. CXI, Abt. 1, p. 69.

[2] Thus for instance, R. Kraus, Gr., Stoffwechsel bei den Crassulaceen. Abhandl. der Naturforsch. Ges. Halle, Bd. XVI. Timpe, Beitr. z. Kenntn. d. Panachierung. Diss. Göttingen, 1900. Tschirch, in Bot. Cbl., 1887, Bd. XXXII, p. 94. Kassner, Ueber Solanin in Kartoffeln. D. Landwirtsch. Presse, 1887, Nr. 19. (Just's Jahresber., Bd. XV, 2, p. 340). Strasburger, Ueb. Verwachsungen u. deren Folgen. Ber. d. D. Bot. Ges., 1885, Bd. III, p. XXXIV. Sauvageau, Infl. d'un parasite sur les plantes hospitalieres. C. R. Acad. Sc. Paris, 1900, T. CXXX, p. 143. Ritzema, Bos, Over het ontstaan van giftstoffen in plantedeelen die door parasitische schwammen zijn aangetast etc. Hygien. Bladen, 1901, Nr. 1-3 (Zeitschr. f. Pflanzenkrankh., 1902, Bd. XII, p. 235). On oxidation enzymes, compare above p. 35, note (1). Mangin, S. la constitution d. cystolithes et d. membr. incrustees de carb. de chaux. C. R. Acad. Sc. Paris, 1892, T. CXV, p. 260. Boodle. On lignification in the phloem of Helianthus annuus, Ann. of Bot., 1902, Vol. XVI, p. 180. Compare also above p. 64. Koycheff, Infl. d. blessures s. la formation d. matieres proteiques non digestibles. Rev. gen. de Bot., 1902, T. XIV, p. 449.

GENERAL OBSERVATIONS ON THE ETIOLOGY AND DEVELOPMENT OF PATHOLOGICAL PLANT TISSUES. DISCUSSIONS OF GENERAL PATHOLOGY. THEORETICAL MATTER

In the present, and concluding chapter we will recapitulate the results already attained, arranging them according to diferent general points of view. In this, opportunity will be offered for making reports on many important matters which at the time had to be left unconsidered.

The diversity of the forms disclosed by the study of plant pathology is extraordinarily large. We find among representatives of the same species, that leaves, which under normal conditions, are developed into extensive thin sheets of tissue, may under abnormal conditions occur in the form of slender insignificant scales, or swell out to fleshy tissue cushions; instead of a large leaf-blade and a short petiole, we find that a tiny blade may appear on an immensely lengthened stem, or the leaf may be covered with very different kinds of swellings, or it may be transformed into a single massive lump, which can be termed "leaf" only because of its position on the plant body and the like. Hand in hand with these macroscopically noticeable differences come variations in anatomical structure. While, in normally developed leaves of one and the same species, the same structural conditions are always recognizable in cross and surface sections, abnormal examples show very great differences, according to the nature of the disease. The repertoire of structures is inconceivably extensive, especially in hyperplasias, produced by the action of foreign organisms on leaves and other organs. The capacity for diverse and brightly colored forms possessed by the cells which make up the leaves is astonishing;- a consider-
(267) ation of exclusively normal forms and structures would not lead one to imagine such a diversity. We recognize the fact that m many courses are possible for the developmental progress of the cells or cell groups and the question forces itself upon us;- what factors decide which one of the many possibilities shall ultimately be realized. It will be necessary to ask, for example, why the cells composing the primordial leaf, do not furnish those derivatives in the process of division which we are accustomed to find as normal components of "healthy" leaves;- or <u>why</u>, in some cases, besides the normal cells, still others are produced, which have some abnormal characteristics. Obviously the action of variable factors is reflected in these distinctly different forms, which factors act on definite kinds of cells and thus influence the formative processes. Before taking up the study of the factors at work and of their action, some general remarks might be useful by way of introduction.

Without doubt, processes and qualities noticed in organisms and in portions of organisms are influenced by very different kinds of factors, to a still greater degree, than are those of inanimate bodies. Various kinds of forces change the cells and tissues in the most diverse ways. Mechanical pressure and strain mould the form differently, loss of water through diosmosis or evaporation decreases the volume, increases the concentration of cell solutions containing water, changes the ormotic pressure and so forth. Besides changes and effects of this kind and similar ones, still others of unequally greater importance come under consideration, which are not sufficiently explained by the transversion of the amounts of energy supplied. While in the above mentioned processes of changes in energy equal amounts came into play in cause and effect, we must consider those processes and effects, in which there is a very noticeable disproportion between the amount of energy furnished by the stimulation and that expended in the effect, on the part of the cell: In this indeed the amount of energy expended by the cell is larger than that brought to it. We will term an effect of the kind first named, the force effect, one of the second kind the stimulus effect. The energy supplied can affect the organism in both ways. While the force effect is independent of the energetic condition of the cell, no stimulus effect can be produced without a sufficient and available amount of potential energy, which, in the process of stimulation, can be transmitted by the cell into actual energy. Each stimulus effect is therefore dependent first of all on the energetic condition of the cell and may in this sense be considered as having been accomplished by the cell itself.

Although the above-said makes clear the principal difference between the force effect and the stimulus effect it will not always be possible, when judging of single processes, to decide which class of effect is concerned in each. If, for example, a cell divides, under the influence of any factors whatever, we will not be able to say whether the amount of energy furnished is equal to that expended in the process named or not. Such difficulties confront us also when judging of almost all the remaining processes of growth and formation. Since in this treat-
(268) ise these processes of growth and formation are concerned, it will therefore be advisable in the use of the word "stimulus effect" to make ourselves independent of any considerations regarding energy and its use and, with Herbst[1], to speak of stimulus effect in all those cases in which any cause whatever "may induce a resulting phenomenon in some living organism", - "because of the unexpected character which these resulting phenomena always have". Accordingly, we will venture to speak of force effects only when we can understand in terms of energy the ones observed on the organism or when they make possible conclusions as to the proportionate amounts of energy and in so far have no longer any "unexpected quality". Stimulus effect takes place in almost every case with which we shall be occupied: all processes of growth and differentiation are the reaction of the living organisms to some stimulus[2].

Various types of stimulus effect may be distinguished, according to the nature of the stimulating agent as well as to the character of the reaction to the stimulus.

Every occurrence in animate as in inanimate nature involves some change. We can, however, think of changes of all kinds only as being brought about as the result and effect of some other change. Also, each process of formation and differentiation may not be imagined otherwise than as the effect of some change in one of the many factors influencing the cell life.

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[1] Ueber die Bedeutung d. Reizphysiologie etc. 2. Tl. Biolog. Cbl., 1895, Bd. XV, p. 721.

[2] It is possible that with a better knowledge of cell physiology and the mechanics of the protoplasm, many a "stimulus effect" will lose its, to us, "unexpected" character and will be shown possibly as a force effect. We are at present very far indeed from having this insight into cell life.

The effective factors, in which any alteration becomes the cause of stimulation, lie either in the outer world or are produced in the interior of the organism by the activity of the cells themselves. Accordingly, external and internal factors must be distinguished:- in their action, we speak of external and internal stimuli.

Fungus spores germinate when placed in a nutrient solution; a small germ tube growing out of the roundish spore. This phenomenon of growth and change of form is caused by the alteration in the conditions, to the action of which the spores are exposed. Contact with the nutrient fluid and even more the endosmotic absorption of water and nutritive substances, act as stimuli, the reaction of which is recognizable in the phenomena of germination. If the short germinating tube is left under similar conditions, still further change takes place; the small germinating thread becomes steadily larger and is divided by cross-walls into several cells. These formative processes are also stimulus effects, to be sure, the external conditions have not been changed, but the factors acting on the cells themselves are different. Each enlargement of the germ tube results in changes in it which may be found in a displacement of the separate particles, in changes of the chemical
(269) nature of the cell contents, variations in circulation and osmotic pressure, in changes of tension conditions etc. The continuous alteration in the internal factors furnishes an uninterrupted chain of stimuli to which the organism responds equally uninterruptedly with typical reactions. If we resolve the processes of development of the growing germ tube into innumerable differentials, each of these represents the reaction to a definite stimulus; their sum furnishes a continuous process of growth and formation.

Formative processes - among which we must unconditionally include the continuance of a process of growth, which has begun already - can therefore result from external as well as internal stimuli. Without a change in some factor, - external or internal - no process of growth and formation is conceivable;- nothing is produced "of itself", nor does it change "of itself".

Even if the beginning of a process of growth, just as its continuance, be conceived of as due to the stimulus effect, still an essential difference exists between the two processes. We will wish to mark this difference by terming "rectipetive stimuli" those which cause the continuation of formative processes already begun, and formative or morphogenic[1], the ones which qualitatively introduce new formative processes. Justification of this distinction may be found in the importance of the latter in the maturing of animals and plants. On the other hand, the near relationship between rectipetive and formative stimuli of formation are involved; they are all formative in the broadest sense of the word. In rectipetive processes of stimulation, the stimulatory cause apparently lies in the changes in internal factors; in the formative ones it must usually be sought for in a change in the coöperative action of external factors. Without any change in the internal and external factors; i. e. without some stimulus - this must be re-emphasized - neither a rectipetive nor a formative process of growth is conceivable.

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[1] On this word compare Virchow, Ueber Reizung and Erizbarkeit. Sein Archiv. 1858, Bd. XIV, p. 1. Billroth, Ueb. d. Einwirk. lebender Pflanzen- und Tierzellen aufeinander. Wien 1890. Herbst, loc. cit.

In the broad meaning which we have given to the conception of stimulation we will have to include also as s stimulus effects those processes of growth, which, according to Weigert[1] and numerous other pathologists, can not be traced back to the action of a formative stimulus, but which are caused by the removal of any kind of hinderances to growth. According to Weigert we are concerned in all abnormal tissue proliferation with phenomena of growth etc. made impossible under normal conditions of life and a normal cause of development by all kinds of impediments. The removal of any opposition is evidently equivalent to the change in the effective factors, (external and internal). According to our definition of the processes of stimulation
(270) and its causes, no reason exists for explaining the effects of growth which are caused by the removal of impediments, as other than the stimulus effects.

We will soon return to the question as to whether there are normal plant tissues of which the formation may be explained by the removal of any opposition to growth.

We have termed stimulus the change in any active factor, but not every change of external conditions causes reaction on the part of the cells,- many a change, which acts as a cause of stimulation in definite kinds of cells, does not come into question at all as such in cells of a different nature. In short,- each reaction presupposes a definite qualification of the cells,- without a capacity for reaction there is no reaction.

The spores of the fern usually germinate very quickly when strewn on a nutrient solution,- provided they are exposed to the light. The spores react by growth to the stimulus brought about by the absorption of food stuffs, after the light has made the cells capable of reaction. As has been shown, in this case the capacity of the cells for reaction may be brought about also by increases of temperature[2]. The spores of mosses feel this same necessity for light,- in them, this capacity for reaction can also be produced[3] by a supplying with sugar. In most cases we find that the reaction capacity of the cells is dependent on definite conditions. The supplying of energy is supposedly the chief cause in its production, and then follows the consumption of energy in the reaction to stimulation. It should be observed here that the energy supplied from without is not convertible in every form for the cells, nor transvertible into potential energy.

Distinction must be made between an accidental incapacity for reaction, explained by a temporary lack of potential energy, and a specific incapacity remaining peculiar even to the cells which are provided with potential energy. While definite changes in the factors cause stimulation reactions in definite kinds of

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1 Neue Fragestellungen in der pathologischen Anatomie. Ges. deutscher Naturf. u. Aerzte, Verhandl. 1896.

2 Forest Heald, Gametophytic Regeneration, Leipzig, 1897.

3 Further examples on the "preparatory" influence of light and other factors in Klebs, Beding. d. Fortpfl. bei einigen Algen u. Pilzen, 1896.

cells, they remain ineffective in others,- these cells do not react to that kind of stimulus. Like so many other phenomena, we will not be able to explain capacity and incapacity for reaction in other way than by the assumption of a specific nature of the cells which may be based on structural conditions, chemical peculiarities, phenomena of tension and of movement in the cytoplasm and the cohesive and adhesive action of its molecules. Not only do cells of various plant species behave differently in regard to this capacity for reaction, but even the cells of various organs and tissue forms in the same species and the cells of different ages. In any case we will have to locate the causes of each reaction or non-reaction in the cytoplasm. Each formative process is caused by the specific peculiarities of the cytoplasm, set free or brought about by a change in some internal or external factors.

(271) Like everything that happens, we can not picture to ourselves all formative processes as otherwise than casually conditions - which holds good for the variously changing pathological formative processes as well as for the normal ones which in corresponding organs in the same plant species always lead to well-known structures. Each formative process is caused by the specific quality of the cytoplasm and by the sum of all the active factors, which bring about the separate processes of formation. The mixed kingdom of normal and abnormal forms is thus far a well-ordered one; the opposite is inconceivable. Each separate process takes place as a matter of necessiry and is the only one possible under the conditions just then in control. The enormous diversity among abnotmal forms can not lead us astray here,- just as for the locomotive, when travelling over a much branched network of rails, there is only one way possible, which is determined by the sum of all the effective factors,- in this case, by the placing of the switches.

If, in comparing normal and abnormal tissue forms, we speak of "arrested developments", of a "tendency" to differentiation, which "exceeds" the normal degree and kind of tissue differentiation and so forth, these are all expressions which are of course meant only figuratively and have been chosen because of their vividness. In the firm causal system represented by the course of development of an organism, there is no room for special "tendencies" of the cells and tissues toward any particular method of development. Where, however, no tendency exists, we can also speak only figuratively of any "arrestment". There is no "normal" and "abnormal", no "tendency" and no "arrestment" for the organism which does not "strive" for any special ("normal") method of development, but, as a natural body without will power, is formed just as the sum of the external and internal factors may determine absolutely. Yet the introduction of such terms is necessary in our work since we can obtain clearness, and be understood only by a comparison of the diverse forms and processes among themselves and by the establishing of a norm, by which we attempt to standardize all.

After these introductory remarks, it will be our task in that which follows, to ascertain and analyse so far as possible the factors active in abnormal tissue formation; we will further have to consider the reaction to stimulation, the abnormal formative processes, from general points of view and then finally test the capacity for reaction in various plants and plant tissues to response to definite stimuli.

All abnormal processes of growth amd formation in plants are obviously caused by definite external life-conditions. In the present section we will attempt to mention by name those factors which become influential in the formation of plant tissues and can cause the production of abnormal forms,- and also to study the way they act. The science to which we will endeavor to furnish some contributions by considerations of this (274) kind, has been called, since Roux, the developmental mechanics of organisms.

We will encounter many difficulties when busied with this task,- so that it is advisable to become closely acquainted with them from the beginning.

In the "introduction" mention was made of the fact that the investigator who works experimentally, will find himself, in a favorable position for the "study" abnormal plant tissues, since it is now possible to produce artificially and at will most of the forms of abnormal plant tissues. We will not deceive ourselves, however, with the thought that we can experimentally cause definite processes to take place without having some knowledge of the factors actually at work:- Even when we have recognized definite factors as participants in the production of any processes, it is especially difficult to ascertain the specific action of each of these factors separately and to distinguish it from that of the other active factors.

Callus tissues furnish a good example of this. As is well-known, they are produced "after injury". But in this, nothing has been said about the active factors. Obviously, at the time of injury, definite cells and tissues are freed from the pressure of their turgid neighbors. Therefore, the conditions of strain and pressure are changed by the injury. If plants and plant organs are involved, which are not covered with water, the part of the plant exposed will undoubtedly lose more water thru transpiration after the injury than before it. The osmotic pressure in the exposed cells and tissues will be changed, the diosmotic exchange of substances from cell to cell being influenced thereby. Further, in the cells at the edge of the injury, the cytoplasmic fragments and the products of decomposition from the destroyed, dead adjacent elements will exert chemical actions, while contact with the new medium,- air or water - will have an unusual influence on the exposed cells. It should be recalled, from the earlier discussion, that each of the factors here named can also have great influence on the tissue formation of the plants. Therefore, it seems very possible that they are also significant in the formation of callus tissues. How shall we isolate, however, the different factors from one another, in the case of injury to the object under experimentation and ascertain their specific method of effect in the comparative experiments? Our present methods do not always make it possible to carry through this isolation experimentally. Besides, even with the methods now at our disposal, there still remains much to be investigated. At present we do not know what is the significance of the above enumerated factors in the formation of callus, nor whether perhaps the essential ones are still unnamed.

The conditions in many galls are even more complicated. Many of those which we have termed prosoplasmas have been pro-

duced after injury.- Yet the chief factor in their production belongs undoubtedly to the poisonous matter produced by the
(273) gall animals. Besides the factors which hypothetically are to be considered in callus tissues, the action of some special poison will have to be reckoned with, when analysing the "gall-stimuli"[1].

A comparison of the above-named tissue forms with the kataplasmas already described leads to new considerations. I sought to bring forward proof that kataplasmas correspond histologically in all essentials, often indeed in all details, with wound tissues, (callus, wound-wood). Therefore the interference proceeding from the infecting organisms and the conditions under which the tissue of the host plant is brought by those interferences are not forthwith to be put on an equality with the ones which, in coarse injuries and mutilation of the plant body, result in the formation of wound tissue . When, forexample, a fungus grows in some plant tissue and incites it to the formation of abnormal excrescences, corresponding in every way with those produced after injury, the reason for their formation can scarcely be caused by changed transpiratory conditions. At any rate, in many cases one can not speak of the chemical action of dead cytoplasm nor of any product of decomposition,- and it is certainly not probable that changes take place in the mechanical action of pressure and incite the growth of the abnormal tissue in the kataplasmas produced by sucking parasites which live superficially. (Hemiptera). The contact of the inner layers of tissue with atmospheric air should be taken into consideration as a contributing factor in the production of this kind of Zoocecidia and Phytocecidia. Hence the question follows, as to whether factors of different kinds can incite the formation of similar kinds of tissues, or whether perhaps injury and infection make possible to the same extent the action of certain factors, not found among those enumerated above and of whose quality we can not as yet form any decision.

Formative processes simpler than those named here seem well suited for explaining more particularly that which was discussed above.

I would call attention first of all to Kleb's observations according to which it is possible to incite Vaucheria tubes to the formation of zoospores by various kinds of interference. Further, I would pefer to the deformation of fungus hyphae and the like, described above (p.); abnormal processes of growth take place if the concentration of the surrounding medium changes, if fluctuations in temperature become effective, or if a parasite in the interior of the cell, robs it of part of its nutritive substances and so forth. We can either assume, in relation to the question as to effective factors, that external conditions of different kinds are able forthwith to bring about the same effect in the cell, and that the cell responds to unlike stimuli with the same reaction,- or that, disregarding their diversity, external factors directly accessible for our consideration and measurement result in the same conditions, which would come under consideration only as causes of stimulation and bring about the phenomena of reaction studied here. If we could ascertain the active factors, we must grasp the fact that be-
(274) tween the change in factors proved in the experiment and the

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[1] Compare also statement below under 5.

reaction to stimulus observed in the cells, numerous different transitional stages can be made possible. One or more of these transitional stages can represent reactions to stimuli on preceding ones, others can not be understood as due to stimulus effect (in the above discussed sense), but as the effect of the force of the energy supplied. The detailed knowledge of these "chains of stimuli", whose end links in these cases represent processes of growth or formation, is still absolutely closed to us;- in only a few cases are we at present in a position to name a few links of the problematic chain of stimuli and to make probable any causal connection. The numerous works whose authors have taken up experimentally the questions of pathological plant anatomy, often throw much light on the question as to how plants can be brought to a production of these or those tissue forms. But any further dissection of the active factors and the course of their action has been attempted only in exceptional cases and not always successfully.

If we find in an experiment that similar formations of tissue are produced through the action of unlike factors, from what has been said already, we will have to make tests as to whether possibly a dissimilarity of the effective factors has only seemed to exist here, because of our scanty knowledge of the so-called "chain of stimulation", or whether, by more exact proof, similar effects and reactions may not become traceable back to similar causes. Only when a positive answer to this question has been proved impossible, will we admit the supposition, that stimuli of different kinds can bring about similar formation reactions.

When plants cultivated in the dark display tissue hypoplasia, as do those examples which are matured under water or in a scarcity of carbon dioxide, we do not venture to find in this a specific action of scarcity of light or of contact with water etc., but must look for the cause of the hypoplasia in the tertium comparationis, in insufficient nutrition, to the results of which, the non-assimilating and weakly or non-transpiring plants are equally exposed. If fluctuations in temperature and changes in the concentration of the surrounding medium cause the same abnormal processes of growth, we do not find in them any specific action of the temperature or the solution as then present, but must think of the fluctuations of turgor and of osmotic pressure, caused by the changes in temperature and concentration, we must seek in them the cause of the described processes of growth. If the same tissues are formed after the mutilation of parts of plants, as after the infection by fungi etc. the question confronts us as to whether there may not exist factors,- causally conditioned by injury or infection,- which in this case as in that become effective and cause in both, apparently dissimilar, cases the known reactions on the part of the organism. Since our scant knowledge of the effective methods of external factors and the capacity for reaction of cells and tissues for the present makes possible the giving of any satisfactory answer only in a few cases, naturally nothing can be said against the justification in principle of my interrogation.

(275) Since we tract certain kinds of arrestment formations back to insufficient nutrition and recognize in the fluctuations of osmotic pressure the cause of certain abnormal phenomena of growth and the like, we thus become acquainted with <u>specific</u>

causes for certain abnormal formative processes. The fact that very different methods of experimentation allow the same specific cause to come into action makes necessary a differentiation between the means used by the experimentor and the specific causal factors, when judging of each abnormal formation.

The demands made herewith in the treatment of developmental-mechanical questions have as yet been only incompletely satisfied. Our knowledge of cell-physiology is proved to be insufficient in every way. We can let our glance wander over a mighty field of work, which begins to be passable in only a few paths.

We will now pass over to the special discussion of the different active factors and will briefly explain the special form of their action by a number of examples.

1. Influence of Mechanical Pressure and Strain

The effect of mechanical pressure and strain on living plants and especially on the formation of tissue, may be considered from different points of view.

Force effect alone is present, when, for example, through pressure, the elements of a tissue are changed from their normal position and are twisted and bent. Tissue characterized by such twisted cells are discussed on p. 177. Again, force effect is present when the elements, attacked during growth, are kept from further enlargement. The inhibition of growth alone naturally does not of itself cause the formation of abnormally constructed tissue. If the cell division continues its course in arrested growth, abnormally small-celled tissue is produced. In fact such may be produced, when (by means of a plaster bandage) the objects under investigation are subjected to a sufficiently strong pressure (see above p. 29).

Thus we are concerned with stimulus effect, not only when, by mechanical pressure and strain the cells are incited to growth or division or special processes of differentiation, but also when certain formative processes are in any way influenced in their direction by the factors mechanically effective.

Examples of this directive influence of pressure and strain will be found in Kny's reports. Under the influence of mechanical pressure the meristem cells of the medullary rays in branches of Salix and Aesculus divide in a different direction than under normal conditions. Double rowed medullary rays are produced[1]. It seems to me that a case studied by Klebs belongs
(276) here (fig. 56). If the walls of the cells of Hormidium are made incapable of any further surface growth (by treatment with Congo red), abnormal effects of pressure will be exercised on the growing protoplasts which are enclosed by them. It is very probable that these abnormal pressure conditions cause the abnormal direction of the new cross-walls[2]. It does not seem

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[1] Ueber den Einfluss von Druck u. Zug. u. s. w. Pringsheim's Jahrb. f. wiss. Bot., 1901, Bd. XXXVII, p. 55.

[2] Compare also above p. 160.

impossible that, in the above named "stimulus effect" and similar ones, some are concerned which later may be recognized as force effects, when the knowledge of the mechanics of protoplasmas and of the physiology of cells has become more exact.

That cells may be incited by mechanical pressure and strain to definite processes of growth, division and differentiation, is proved by the phenomena of so-called passive growth, by cambial cells brought to cross-division by strong pressure and by the cell division which Kny found in the pith of Impatiens and others under the influence of pressure. Further, attention is again called to the activity of hyperplasia of mechanical tissue (compare p. 141).

Thouvenin has shown (compare p. 48) that definite processes of differentiation can be made impossible under the influence of mechanical factors.

> We mentioned above (p. 269) the influence, which, according to Weigert and others, is exerted upon tissue-formation by the removal of hinderances to growth. The consideration of the action of mechanical factors is of the greatest importance here and, in fact, Ribbert[1] has recently attempted to explain very different forms of pathological growth - regeneration, inflamation, formation of tumors - by the removal of mechanical hinderance to growth.
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> So far as the formation of abnormal plant tissues is concerned, not one of their many forms have been sufficiently explained as yet by an omission of hinderances to growth. It may be stated as very probable that in the production of callus, wound-wood, and others, the removal of bark pressure and similar hinderances to growth is not without influence on the formation of the wound tissue. However, there is no necessity for the assumption, that the removal of the pressure effect causes the formation of wound tissue. We may find an outgrowth of tissues of very different kinds even without previous injury or release from pressure and also of many excrescences (those produced endogenously,- such as galls and intumescences).

2. Temperature

All life-processes, and also processes of formation and differentiation, like many physiological or chemical ones, can be carried through only within certain temperature limits. The formation of tissue on the growing shoots and roots will be discontinued if the temperature falls below the requisite min-
(277) imum or if it rises above the admissible maximum. But the same temperature limits do not hold good for all processes of formation and differentiation taking place in a growing organ or organism. Certain processes may still take place, although others have already become impossible. If unfavorable temperature conditions make certain processes of differentiation impossible for developing tissue, "incomplete" abnormal tissues are produced (hyperplasias). In many plants, formation of the chlorophyll is rendered impossible by too low a temperature (p. 36). Hans found that the formation of cross-walls in growing cells of

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[1] Lehrb. d. allg. Pathologie, 1901.

Bacterium Pasteurianum was omitted when the temperature was too high (p. 71). Thus the living cytoplasm can permanently forfeit its activity for certain processes, as in our first example, or its capacity for reaction to certain (external and internal) stimuli is again made possible so soon as the disturbing effects of the unsuitable temperature are removed - as in our second example (see above).

No absolutely certain case is known as yet in which abnormal temperature conditions can cause the formation of abnormal tissue in any way other than by the arrestment of certain processes. In Prillieux's experiments (see above p. 89) the arresting action of a high degree of warmth seems to combine with the action of air which is free from water vapor. As regards the observation, that abnormal cell-division occurs in many fungi at high temperatures, it seems to me that we are still insufficiently oriented as to the disarticulating action of temperature.

3. Light

The influence of light on the formation of tissue is at any rate slight, since no specific effects of this form of energy are known.

It was demonstrated that illumination can cause the formation of chlorophyll and anthocyanin and that the formation of pigment is often lacking in the dark. But since it was shown that the formation of chlorophyll (in various algae) is possible even in the dark, when certain nutritive substances are added and that, in the same way, cells can be incited to a formation of anthocyanin independent of light or darkness,- we may assume that the formation of pigment after illumination does not represent a very specific action of light, but that it is caused by nutritive conditions, the production of which is made possible in the cells by theinfluence of the light.

If the tissues in etiolated plants reach only a moderate degree of differentiation, while the individual cells often become larger than under normal conditions, we may not see in this any specific result of a lack of light, but the effect of scanty nutrition and reduced transpiration. We observe the same tissue changes in examples which are raised in the light in a damp room that we find in cultures made in the dark.

The question as to whether continued illumination can "arrest" certain formative processes, as seems to follow from Bonnier's experiments (see above p. 57), needs closer investigation.

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4. Chemical Substances

So far as any insight into the factors which are effective in the formation of tissue is possible in the present state of our knowledge, we may indeed maintain, that the great majority of the processes of growth, formation and differentiation are brought about by stimuli given out by chemical substances.

Without doubt, each process of growth, etc. presupposes the presence of certain substances, no matter whether they are supplied to the cells from without or are produced in them autochthonously by assimilation. If these substances are lacking, or are present in insufficient amounts, certain processes of growth and formation are omitted and "arrestment forms" are produced.

If the cells are over-abundantly provided with those substances, many processes of growth and formation may in one way or another be continued beyond the normal standard. However, it will scarcely be possible to decide in a single case as to whether the nutritive substances act as stimulation causes or whether the cells are not rather given the capacity for reaction by these substances, in order to react, in the way described, to any stimulation causes which as yet have been discovered.

In some cases we may now conclude that most probably the supplying of nutritive substances has only some "preparatory" action. Roux has shown that the hypertrophy of activity in man and animals can not be a reaction to functional hyperaemia (and the supplying of nutritive substances connected with it) but is to be understood as a specific effect of the increased demand[1]. The same conditions exist for the activity hyperplasias of mechanical plant tissues described above. The supplying of nutritive substances, which certainly precedes their formation, apparently only makes the tissues capable of reacting in the above described way to stimuli of a definite kind;- in the present case to mechanical strain and pressure. The actual freeing momentum does not lie in the supplying of nutritive substances but in the action of mechanical factors;- hence the necessity of mentioning activity hyperplasias under 1. If we find that definite formations of tissue occur after the supplying of nutritive substances, it will be necessary, even when no other factors may be found to be the cause of stimulation, to think of the possibility that the supplying of nutritive substances is effective only as a preparation,- not as a setting free,- and that the f factors which do set free are still unknown. I will return at once to this point.

The action of oxygen and water is exclusively preparatory. Among the cases, which are of interest to us, not one can be found in which a freeing stimulus proceeds from the supplying of oxygen[2]. The numerous cases in which the supplying of water acts releasingly will be discussed in another sub-division because
(279) in them apparently the water does not act as a nutritive substance, being effective only because of its physical qualities, not at all because of its chemical ones.

The conditions are much clearer when the effective substances are not nutritive ones, but are poisons, which incite the cells to some activity without themselves furnishing any building material. We may assume that no "preparatory" effect proceeds from them, but a freeing one.

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[1] Roux, Der züchtende Kampf der Teile in Organisms, 1881. Ges. Abhandl. Bd. 1, p. 315 ff.

[2] That, under certain conditions, the supply of oxygen may also bring into existence directly or indirectly, releasing effects is shown by Natzuschita's investigations on anaerobic bacteria, which form spores under the influence of oxygen. (Zur Phys. der Sporenbildung d. Bacillen etc. Dissertation Halle, 1902, Arch. f. Hyg., 1902, Bd. XLIII, p. 267).

Some cases will be discussed later, in which the action of nutritive and poisonous substances and their trophic and toxic effects will be illustrated. As said above, in many cases it must remain undecided for the present in trophic action, whether a freeing or a preparatory influence of the living cells and tissues is involved here.

Trophic effects, varying from the normal are produced in various ways,- an insufficient supply of nutritive substances causes hypoplasia, while an over abundant one leads to hypertrophy or hyperplasia.

An hypoplastic formation of cells and tissues always occurs when insufficient amounts of nutritive substances lie at the disposal of the organisms or of its separate parts,- or the composition of the food stuffs offered does not supply the substances required for a normal development. We observed hypoplasia in plants which live in the dark or in places free from carbon dioxid, which therefore by assimilation can not produce from themselves the necessary amount of nutritive substances; further, in those plants, in which transpiration is arrested by cultivation under water or in moist places as well as by the exclusion of light, and whose transpiratory current is therefore too weak to supply the needed amount of nutritive substances to the different parts of the organism. "Shade-leaves" are also to be considered in this connection. It must remain doubtful whether in the production of galls bearing the character of hypoplasias, the giving up of nutritive material to the parasite which produces the gall may play the chief part or not. We can further observe hypoplasia in plants, which must support their existence without iron, calcium or other "indispensable" substances. The conditions in the homoeoplastic excrescences of the sugar beet already described (p. 139) are more complicated. New formations are produced, which apparently use up all the available amounts of nutritive substances, so that the neighboring tissues seem to be arrested developmentally. The "struggle of the parts of the organism" leads here to a "correlation hyperplasia"[1].

A continuance of the processes of growth and differentiation is produced by trophic influences when the cells are brought, by some means, to the production of substances without which cer-
(280) tain processes can not take place. The formation of chlorophyll is clearly dependent on some unknown substances, which in most plants are produced in the cells themselves only under the influence of light. Many algae, however, are known to form chlorophyll in the dark, after having been supplied with organic nutriment and it seems not at all impossible that future investigations

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[1] At times, in the formation of "semi"-annual rings, we have to do with the same phenomenon (p. 25). Further in the observations of Elfying (loc. cit.) who found in bent inflorescence-stalks that the collenchyma was formed abnormally abundantly on the convex side, but was retarded on the concave side. Still, it is undeniable that in the last named case, still other constructions are obvious. I refer further to that said above (p. 140) for Aristolochia-ridges (Observations by Magnus).- If in Erineum galls, the epidermal cells hypertrophy greatly, but the parts of the mesophyll belonging to them, seem arrested in their development (fig. 38), a correlation-hypoplasia may possibly be present; the arrestment, however, can also illustrate the effect of gall-poison.

will make known certain substances by the supplying of which even higher plants will be in a condition to produce chlorophyll in the dark.

We will venture to explain the metaplastic anthocyanin formation in Saxifrage leaves (see above p. 58), the production of correlation-homoeoplasias and heteroplasias[1] and in part also the formation of many callus tissues not by an abnormal new production of nutritive substances but by an abnormal assimulation of substances already present and those produced in the normal course of life-processes. Local accumulation of nutritive substances as a result of abnormally increased transpiration might also be operative in the formation of wound-cork.

No absolutely certain example has been known as yet in which abnormally increased supplying of nutritive substances from without can promote the formation of tissue beyond the normal amount. Arrestment phrnomena seem rather to be caused by abnormally increased transpiration which accelerates the transpiratory current, as is shown by dwarf examples in dry habitats. As yet, at any rate, no normal formation of tissue has been incited by an artificial supplying of organic nutrition from without,- yet it is to be hoped that the experiments recently made by Haberlandt and Winkler on isolated plant cells will lead in the future to positive result s.

Toxic effects, consisting of degeneration changes of the cell, may be left unconsidered, Those cases are important for us, in which an arrestment or a promotion of certain processes is noticeable after the action of any poison.

Arrestment may be brought about by very different kinds of substances. Some, taken up by the plants in small doses as food stuff and there worked over, can act as "poisons" when used in greater amounts. Mention must be made here also of the arresting effect of organic food in green flagellates, diatoms and others, which become 'apochlorotic' under the influence of an abnormally
(281) abundant supplying of nutritive substances. Farmer and Chandler (see above p. 48) have made reports on the arresting influence of air which abounds in carbon dioxid. In order to arrest the

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[1] The formation of correlation-homoeoplasias and heteropasias belongs among those cases of abnormal tissue production, in which the abnormal supply of material does not act releasingly perhaps, but only as a preparation or as a qualifying effect. If any cambium or any parenchyma capable of division, under the influence of the supply of food stuff, continues longer the production of cells and acts more intensively than under normal conditions, the releasing agent may well be sought in "internal" factors. Similar but more complicated examples are discussed with the same point of view by Driesch (Die organischen Regulationen, Leipzig, 1901, p. 118). I share completely his interpretation of this matter. It is difficult to answer the question, as to what factors in hyperplastic formation of vascular bundles in dahlia tubers (Vöchting's experiments) act releasingly as a result of increased demand upon them (Activity-hyperplasia, see above p. 146), whether, perhaps in this case, the intensity of the current, i. e. something mechanical, caused the stimulus (Driesch loc. cit.) or whether here also only "internal" factors were at work and the intensive current of food stuff created only the necessary nutritive condition, the desired ability to react.

process of cell-division, Garassimoff used substances which act as "poisons" in every concentration and under all circumstances. It is possible to produce successfully asporogenic "races" in different kinds of bacteria, by treatment with various acids (hydrochloric, rosol and carbolic acids)[1].

The exciting effects of poisons becomes noticeable therefore when it is possible to increase the growth intensity of lower or higher plants by treatment with anaesthetics or metallic compounds. Abnormal tissue formation as a result of the exciting action of toxic substances has been repeatedly described above. Poisons produced by necrotic decomposition of the cells and tissues seem able, under certain conditions, to incite the formation of wound-cork and wound-wood. As Winkler has shown (see above p. 98) foreign substances, supplied from without, are able to incite cell-division. Finally the action of poisons is also the cause of gall formations,- such as, for instance, all prosoplasmas.

5. Turgor, Osmotic Pressure and Diffusion-Currents

The significance of water in the processes of cell growth and tissue formation lies especially in the fact that all these processes are possible only when a definite amount of water is present. The "preparatory" action, proceeding from a supplying of water and its absorption, is unmistakable. Only with a definite degree of turgor do the cells become capable of an activity which leads to a normal or to an abnormal formation of tissue. The question as to whether increase or decrease of turgor can set free definite formative processes still remains to be discussed.

In fact, examples are known for an action of this kind due to changes in turgor. I include here especially hyperhydric tissues (compare p. 74). When the amount of water given off by any cell whatever is reduced, the turgor of the cell will be increased by a continued absorption of water. By this abnormally high turgor, the cell is incited to growth-activity, producing long cylindrical tubes, such as those pictured in figures 19, 23 and others. The abnormal amount of water makes possible the stimulus to which the cell reacts with growth[2].

We have named first of all cases in which, by the absorption of water, (the increase of turgor) the cells have been incited to definite action. The question must still be settled, as to whether formative stimuli can also proceed from changes of an opposite kind.

Free-lying cells, like fungus hyphae, root hairs, unicellular forms and the like, are easily accessible for experimentation. Root-hairs are especially useful since they react very easily and quickly to influences of all kinds. The deformations described above (p. 120) and easily produced prove that abnormal processes of growth and set freeeven in a treatment with materials

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[1] Compare for example Behring, Asporog. Milzbrand. Zeitschr. f. Hyg., 1889, Bd. VII.

[2] The interpretation of the authors who speak of the growth as a direct result of turgor ("as a force effect") is erroneous.

(282) which withdraw water,- thus reducing the turgor of the cells, increasing the concentration of their contents and so the osmotic pressure. The hairs grow chiefly in thickness, instead of continuing their normal growth in length. Reinhardt observed the same phenomena (see above) in fungus hyphae. Changes in concentration and composition of the surrounding medium as well as fluctuations in temperature have called forth the same deformations. In both cases we may venture to explain the abnormal forms by fluctuations in turgor and osmotic pressure. In just this connection in my opinion belong the Vaucheria galls of Notommata, the involution forms of bacteria and others.

There is a need of a closer testing of the question as to whether abnormal processes of growth in etiolated plants, the phenomena of "starvation-etiolation" and others, may be explained in the same way, - and further whether hypertrophies, produced after poisoning (gall hypertrophies), may in part at least be understood to be the result of phytical changes in the cell-microcosmos. It may indeed be possible that substances are supplied to the infected plant cells by the parasite, which act on the cell life to the host plant less through their chemical qualities than their physical characteristics and may perhaps cause an abnormally high osmotic pressure within the infected cells. This poijt also will have to be considered in a future analysis of the "gall-stimulus". Let us remember further that any abnormal absorption of water reduces the concentration within the cell, and therefore its osmotic pressure, but that amalogous changes in osmotic pressure are produced not only by the absorption, or the giving off of water, but also by fluctuations in temperature and by chemical transpositions within the cell, in which substances osmotically effective are converted into ineffective ones, or osmotically ineffective substances are changed to effective ones. As is shown, a varying connection exists between the osmotic pressure within the cell and the external conditions of life. A wide field of work lies open here for future investigation. For the present we must limit ourselves to the mention of new questions.

The diffusion currents in the cell body are closely connected with the osmotic pressure within the cell, these I will mention briefly.

The growth of a crystal in its mother solution undoubtedly leads to some changes in the concentration of the solution immediately surrounding the crystal. The changes in concentration for their part result in diffusion-curfents which are definitely directed. Differences in the processes of diffusion and therefore in the conditions necessary for the continuance of growth on the different parts of the crystal will apparently be produced so much the sooner, the greater the amount of the surface of the srystal here concerned. The fact that crystals of definite substances usually continue their "normal" growth only toma certain size,- and then grow "abnormally",- makes it possible to conclude without doubt as to unequal conditions of crystallization on the different parts of the crystal, and we may conceive of some minute "disturbances" in the course of the diffusion currents.

(283) These diffusion currents must be produced in the living cells just as in the crystal-mother-solution, if a crystal or a conglomerate of crystals is produced anywhere in the

cells, or if any soluble substance is gradually carried over into an insoluble compound. Therefore, for example, in the construction of a starch grain, in the growth of a membrane etc., we may now assume that the course of this process of growth becomes irregular when different parts of the growing form are placed under dissimilar conditions of growth, by disturbances in the regular process of diffusion. Without doubt disturbances of this kind occur so much the more easily and cam become so much the more conspicuous, the larger the growing forms are.

It is a noteworthy fact that even in the organic kingdom there exists some connection between abnormal size and abnormal form. Figure 120 gives at B some abnormal giant starch grains from the correlation-heteroplasmas discussed above (p. 152), which Vöchting found in the form of "leaf tubers" in Oxalis crassicaulis. The abnormal grains (B) appear, beside the simple normal ones (A) as bizarre as is possible. "All show peculiar appendages, some short and knob-like, others longer, sometimes long and straight, or again bent like hoods". At times irregular humps are produced, which can fill whole cells. We do not know why starch grains should be come larger in the above-named
(284) abnormal tissues, then under normal conditions. Their abnormal form is caused, I expect, at least in part, by the above discussed differences in the conditions of growth[1].

In a consideration of entire cells, we also often find abnormal forms associated with abnormal size. A well-known example of this is furnished by the involution forms of bacteria, among which are found branched forms, lying next to vesicular or spindle-like ones. The latter are evidently produced by differences in the conditions of growth in different parts of the cell membrane, and by the unlike distribution of substances. The branching will arise ceteris paribus on the places "preferred" - those better provided with building material. The larger the cells, the more easily are produced the described differences in the intra-cellular distribution of substances through disturbance of the diffusion currents.

B. On Reaction to Stimuli

The preceding chapters have contained more detailed reports on the reaction to stimuli of cells and tissues in so far as they consist of processes of growth and differentiation. Only a few general remarks remain to be added to this point.

In the normal course of life of a cell, we find that cell division regularly follows cell growth in such a way that nuclear division and the formation of cross walls takes place as soon as the definite cell size is reached. Evidently, during the growth of the cell, some physical conditions or some chemical substances are produced, which incite the cell body to division. In this process we are concerned with the effects of stimulation action and indeed of internal stimulation, the effective factors being produced by the activity of the cell itself. By means of innumerable examples, pathological plant

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[1] In many, processes of coalescence also may possibly be at work.

anatomy now proves that cell division and growth do not at all represent inseparably linked processes and that the total result of separate processes, which in the normal course of development are constantly repeated in the same way, is capable of very different modification. We can cause cells to divide without previous growth, which under normal conditions, would have been enlarged and then have divided, and conversely can cause their growth without any division taking place. The first experiment is successful, when we take away from the cells the conditions presupposed by growth. Therefore, with previous growth, those factors may also become effective in the cell, which incite division. In experiments of the second kind, we make the cell incapable of reacting normally to these very factors, or we do not allow any of the conditions and substances to appear which incite division. No matter how we may wish to interpret the state of affairs here described, it teaches at any rate that factors leading to division in the cell can also be produced without any previous growth and that conversely division should not be understood to be a physically necessary result of growth which has already taken place, - in other words,
(285) that the phenomenon of cell growth and that of cell-division can occur independently of one another, according to the conditions, which are already effective on the cell and in the cell.

This same "independence" occurs in all other processes of division, the sum of which makes up the development of an organism. In growing root hairs etc., an increase in cell volume keeps pace with the new formation of cell walls. We may arrest the growth and still find that the cellular products continue their course. Cell division and nuclear division are indeed independent of one another. Even in plants, which under normal conditions consist of only unicellular units, multicellular elements are produced under certain circumstances, if for any reason the conditions necessary for the formation of cross-walls are not filled. On the other hand, nuclear division can be "arrested". Just as "independent" as the processes of division just named, are also those which give the cells their characteristic "inner form" and signify all differentiations of cells and tissues. The processes of tissue differentiation, taking place normally after a certain number of cell divisions, can also occur abnormally early, before the normal number of cells is present, or can be lacking even when the usual number has been reached, or indeed exceeded, and the like.

According to the number of processes of division taking part in the formation of various abnormal tissues, we can construct a list beginning with the simplest hypertrophies and ending with the most complicated hyperplasias. Growth of the cells alone was observed in the production of many hyperhydric tissues (kataplastic hypertrophie), growth together with increase of cytoplasm, for instance, in the gall hypertrophies,- growth, cytoplasmic increase and nuclear division lead to the formation of multinuclear giant cells; the same processes together with cross-wall formation may be found taking place in almost all hyperplasias. In the preceding chapter in the discussion of prosoplasmatic galls, it was shown, how diverse are the combinations in which the different kinds of differentiation processes can be united with other processes, the production of which is made possible by a hyperplastic tissue outgrowth, without its being connected with them. We find that lignification takes place in many abnormal tissues after repeated cell division. - The same process is enacted in other cases, however, even without previous enlargement and divisions of the cells concerned. Parenchymatic excrescences of Solanum tuberosum may be produced (according to Vöchting's experiments) even without any deposition in them of the usual starch masses. On the other hand, there are many cases, in which it is found that abundant quantities of starch have been accumulated, without any preceding formation of any excrescence whatever etc.

It has not yet been proved experimentally that all processes actually connected with one another in normal development, so far as time and place are concerned, can assert their "independence" under suitable conditions and can occur independent of those other processes with which they seem to be combined normally. Yet the actual material at hand justifies even now the assumption that all processes of division should be termed "independent" in the meaning here explained. The capa-
(286) city for certain formative and differentiating processes is determined, to be sure, by the special qualities of the cytoplasm of the different plant varieties. The combination in space, however, and the sequence, in which we find the separate processes enacted in a normal course, may be understood as caused by the influence of all effective "internal" and "external" factors, the majority of which are evidently still withheld from our knowledge.

Klebs[1] proved for the lower organisms, in the growth of which relatively few formative processes of division are repeated, that the combination of these takes place quite differently under changing conditions of life and can be modified experimentally at pleasure. That in higher plants only the incompleteness of our knowledge and our methods of experimentation prevent the carrying through of similar experiments is attested to by the results of pathological plant anatomy.

It is now desirable to approach in still another way the point treated here.

If we compare the cells of abnormal tissues with those of normal ones, we will find either complete correspondence (homoeoplasias) or more or less striking differences. The variation of individual cells from the normal is only moderate when the individual cells in one or more ways resemble the undeveloped elements of normal tissues (hypoplasias and many kataplasmas). On the other hand, the differences are often very marked in metaplasia, in prosoplastic hypertrophy and especially in prosoplasmatic galls. The diversity of abnormal cells brings up the question, whether a plant under abnormal conditions can develop other kinds and forms of cells than those which compose the normally developed plant body,- whether the same normal kinds of cells are always repeated in the prosoplasmatic galls, in new and "abnormal" arrangements and combinations.

This question has always been repeatedly asked in the discussion of galls, the most striking of abnormal tissues, and has been answered in different ways.

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[1] Beitr. z. Phys. d. Pflanzenzelle. Tübinger Untersuch. 1888, Bd. II, especially p. 550; Beding. d. Fortpflanz. bei einigen Algen u. Pilzen, Jena 1896, and others.

Göbel, in his "Organographie"[1], states in regards to this, that in galls, neither is anything morphologically new produced, nor any "new tissue elements otherwise not existing in the plants". "New alone are the combinations of the plants' possibilities, the characteristics which furnish the changing pictures of the kaleidospope. Forms transitional between the organs are produced here very abundantly". A note supplements "Cell forms were also found, which do not exist in any undisturbed development, that is, those of the hair formation in "Erineum" galls.
(287) These hair formations, which are caused by mites, are of service to the parasites and vary from the normal hair forms of the plants concerned". Appel[2] seems to share Göbel's view.

Beyerinck[3] holds a different view. According to him "new" cell and tissue forms may indeed be found in galls - at times the representatives of the Tinctoria and Kolleri gall type. Herbst[4], Berthold[5] and others think the same. I have expressed my view as being the same as the authors here named[6].

Of the representatives of the opposite theory, I will name deVries[7]. According to him, galls even of the highest differentiation are composed only of such anatomical elements as are found also in the plants which bear them. "Only the elements of the peculiar stone cell layer in many Cynipides galls[8], which develops later into a thin-walled nutritive tissue, form an exception as yet not entirely explained, which may be only an apparent one".

All other abnormal tissue formations should be investigated from the same points of view as galls.

Berthold (loc. cit.) emphasizes the abnormal structure which may be observable in regeneration and the healing of wounds. Vöchting[9] had already obtained similar results,; he found new kinds of cells produced in wound tissue such as activity-hyperplasias.

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1 Organographie. 1898. Bd. 1, pp. 169, 170.

2 Ueber Phyto- und Zoomorphosen. Königsberg. 1899.

3 Beob. ueber die ersten Entwickelungsphasen einiger Cynipidengallen. Amsterdam, 1882.

4 Ueber die Bedeutung d. Reizphysiologie, 2. Tl., Biolog. Cbl., 1895, Bd. XV, p. 721.

5 Untersuch. zur Phys. der Pflanzl. Organization, 1898, Bd. 1, Einleitung, p. 9. Here also Goebel in Flora, 1899, Bd. LXXXVI, p. 234. Compare also Prillieux, Etude s. la formation et le developp. de quelqu. galles; Ann. Sc. Nat. Bot., 6me Serie, 1876, T. III, p. 135.

6 Beitr. z. Anat. d. Gallen Flora, 1900, Bd. LXXXVII, p. 176 ff.

7 Intracellulare Pangenesis, 1889, p. 117.

8 Compare above p. 254.

9 Ueb. Transplantationen am Pflanzenkörper, 1892; Z. Phys. der Knollengew. Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 1.

The lack of unanimity of these authors is doubtless explained by the present lack of clearness in the interrogation of the phenomena.

It is indeed evident that even unusual hyperplasias like normal parts of plants are composed of cells. The question is, how must the cells be constituted if they may be termed "new" kinds of cells. Evidently the investigators here named have answered this question differently and thus have arrived at different results, in drawing their conclusions. We will first of all be obliged to understand clearly the preliminary question, before taking up once more the oft discussed problem.

"New" qualities, that is, ones which vary from the normal, may be expected to arise in different ways. The conditions of size may be "new", or the forms, or finally the inner structure of the cells. We will therefore have to compare abnormal cells with normal ones, as to size, form and inner structure.

(288) 1. Size of the Cells

Aside from the individual unbranched latex tubes, which seem to be distinguished (theoretically) by unlimited growth, each kind of cell in plants forming tissues possesses a definite size, which is attained early,- and fluctuates only within narrow limits in the individual species.

We have seen above that cells of very different tissue forms may hypertrophy; i. e. may enlarge their volume beyond a normal amounts The question must still be discussed, as to whether the largest cells, to be found in a normally developed plant body, may not perhaps give a maximum cell volume valid for the species concerned, beyond which no cell of any tissue whatever of that species can hypertrophy,- in such a way that, so far as cell size is concerned, the plant can furnish nothing which could not be attained by it also under normal conditions.

The conditions in primitive organisms are most easily surveyed, which, under normal conditions, develop cells of only one size, such as, for instance, bacteria. The often gigantic involution forms of the schizomycetes prove forthwith that, under abnormal conditions, cell-growth can far exceed the normal standard while no definite limits would be recognizable.

p The conditions in higher plants are just the same. In them too we find no support for the assumption that a limiting volume, determined in the plant body, may be determinative for cells grown under abnormal conditions. Figure 121, at the left, illustrates some libriform fibres and pieces of ducts of Quercus at the right some cells of the oak gall produced by Spathegaster baccarum. No further explanation is needed to show that abnormal cells can far exceed the volume of normal ones.

Cells of a tissue under abnormal conditions frequently become appreciably larger than corresponding normal ones; they may more rarely occur appreciably smaller. However, no fixed
(289) boundaries exist also for this lower limit. I will call attention later to the dwarf Desnidiaceae described on page 27, to the ducts of hypoplastically developed plants which have abnormally narrow lumina and to mycelial threads with excessively narrow lumina, which may be found produced in solutions poor in nutritive substances.

To summarize:- In regard to their size, the cells of a plant developing pathologically are not restricted to that which the normal plant may accomplish.

2. Form of the Cell

The form of membraned cells in plants is almost always identical with that of their cellulose covering. The form of the latter is determined by the manner of its production, by conditions of space etc., but especially by the processes of surface growth, which have taken place in the membrane.

The growing cells of a Spirogyra thread remain cylindrical - I follow the supporters of the theory of intus-susception - so long as the newly superimposed particles are deposited equally on all sides and longitudinally between those already present. When a copulatory branch is produced, deposits must have been made on a definite part of the cylindrical wall, longitudinally and tangentially. All changes in form in a growing cell may be traced back to the fact that either new particles of matter have been deposited on every part of the membranes, or only in places; sometimes in one direction, sometimes in several.

If swollen, barrle-like cells are produced on Spirogyra threads, by the action of ether[1] we must assume that new particles have been deposited tangentially and more abundantly in the middle of the cell than at the ends. Therefore, under abnormal conditions differently distributed deposits are made on the cells, whereby other structures are formed than under normal conditions.

A consideration of the deformed root-hairs, fungus hyphae etc. described above (p. 120) is still more instructive. When the hemispherical form of cell ends is persistently retained, during continued growth in length, we may assume with Reinhardt (loc. cit.) that the individual particles of the head are, as a rule, showed toward the outside, until they have reached their ultimate position in the cylindrical mantel and that thereby the deposits of new particles must be most abundant near the long axis, gradually decreasing towards the edge, in order to cease entirely in the cylindrical-mantel". Very marked variations appear under abnormal conditions, club or ball-like forms are produced according to the degree to which the deposits increase tangentially. If the part lying back of the tip grows more strongly than the tip itself, bowl-like forms are produced. If an especially active growth takes place at several different places, branched forms arise and the like. There are indeed no forms which could not be produced by abnormal modification of the surface growth, nor which, under abnormal conditions, have not been found actually occurring in the objects named.

(290) The epidermal cells of leaves and shoots as well as ground tissue cells (fig. 43) can grow out into similar forms as already discussed in chapter IV.

The question as to whether the formal repertoire of normal cells is determinative for deformations which are possible under abnormal conditions, must be answered absolutely in the negative.

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[1] Gerassimoff. Bull. Soc. Imp. Nat. Moscou, 1896, Nr. 3. Nathansohn in Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 65.

I call attention again to the bacteria which developing normally, only become rod-like cells, the involution forms of which, however, seem to have been most diversely swollen, twisted or branched. The form of abnormal cells, as well as their size, has free scope for development which may be said to be unlimited. The noteworthy Erineum hairs (Fig. 40), the two-armed trichon of the gall of Neuroterus numismatis (Fig. 102) and many others prove that the same holds good for higher plants. Under normal conditions cells of this form are never produced on the plants bearing the Erineum nor on the host plant of the numismatis gall.

We can thus affirm that the intensity, the localization, the direction of the membrane growth and thereby the form of the cell, are determined by the sum of all the factors which act (internally and externally) on the cell and that under abnormal conditions "new" cell-forms can actually be produced.

3. Inner Structure of the Cells

Only by considering the inner structure of the cells, will we become acquainted with the limits which, even under abnormal conditions, remain decisive for the development of plant cells.

In the last three chapters, repeated mention was made of the fact that very different kinds of cells, of very different origin, can under certain abnormal conditions assume "foreign" characteristics which often warrant conclusions as to changes in the physiolobical effectiveness of cells. Cells, which remain colorless under normal conditions, develop chloroplasts. Thin-walled cells obtain, through thickenings of their membranes, an especial wall structure; for example, a reticulated one, and so forth. Closer consideration now proves, that an abnormal turning green takes place only in plants which even under normal conditions somewhere develop chloroplasts, that, further, abnormal reticulated wall-thickenings occur only in plants, in which the same formative process is known already in certain normal elements. Therefore peculiarities of the cytoplasm considered as pre-requisites for the formation of chlorophyll, certain wall-thickenings, etc., are not produced "anew" under the influence of certain abnormal conditions, but only become active in those cells and tissues in which, in a normal development the external and internal conditions necessary for chlorophyll formation are not realized. Among others we must consider the nutritive conditions of the cells; in which, therefore, in other words, the cytoplasm for some reason does not "make use" of its capacity for developing chloroplasts etc.

Although the plant, so far as the inner structure of its cells is concerned, even under abnormal conditions, must manage
(291) to live with the same capabilities that are also active in normal development, yet all possible heterogeneous kinds of cells may be produced in such a way that the known processes of differentiation are enacted in the larger or smaller cells, or in those formed otherwise than under normal conditions. I call attention again to the peculiar callus hypertrophies of the Orchids (Fig. 26), to the parenchymatic tracheids in callus tissue (Fig. 67), to branched woody fibres (Fig. 70), to the tracheids which occur at times in prothallia and many others.

It must still be noted that definite processes, known in normal development, can take place with abnormal intensity, more weakly or more strongly than under normal conditions, and further that different parts of the cell can undergo an unequal formation, when the determinative conditions can not become effective in the same way in all parts of the cell.

Under normal conditions, plants, possessing the ability to form sclereids, can produce unusually thin-walled or very thick-walled sclereids; or, stead of cells distended equally on all sides, one-sided ones may be produced etc. To be sure, we know nothing of the causes of the stimulation here effective. But the galls speak in favor of our hypothesis,- at times the Cynipides gall of Quercus, in which we found developed very different kinds of sclereids. The fact has been discussed above in detail (p. 241) that certain kinds of unequally thickened sclereids as well as many other histological characteristics furnish attributes constant for the separate gall forms.

Only an apparent exception to the rule here developed is made by the irregular, sometimes elliptical or spherical, sometimes cone or coral-like wall-thickenings, which are often formed by the action of external disturbances butare absolutely lacking in normal cells of the plant species concerned. I have already referred (Chapter III) to the fact that these thickenings have no definite form and no characteristic structure in so far that all pitting is lacking in them. I would therefore like to assume that this kind of wall-thickening so far as its ultimate form is concerned, is not dependent on definite capabilities of the cytoplasm. Rather, its special qualities seem to have as little to do with the form of the thickenings as they have possibly with the form of the precipitates produced in the cell by the action of external factors. The formation of membrane accumulations, coralloid cones, etc. does not in my opinion make necessary the assumption that newly occurring qualities of the cytoplasm lie at the base of their formation.

On account of the peculiar thickening of their cell walls, (compare p. 211) the threads found in the gall of <u>Ustilago Treubii</u>, which resemble capillitia, are very noticeable. The illustration given out by Solms-Laubach throws no exact light on the nature of these thickenings nor of their production. Doubtless, we will be concerned in their formation only with processes, of which the normal cells are also capable.

As long as it is not possible to cause a turning green of the cells of plants which are free from chlorophyll, of the development of tracheids in the tissue of cell cryptogames so
(292) long as stone cells or wood-fibres are not found in the abnormal tissues of plants which are free from sclereids or stereids, - we may hold to the assumption that in the formation of cells under abnormal conditions, only the "normal" capacities of the cells will come into question and new qualities will never arise. Should anyone ever be so fortunate as to call forth new qualities experimentally, he will thereby solve a phylogenetic question and produce a new species.

So far as is known at present, the varying structures of abnormal tissues are produced by combinations of processes of growth and formation, other than those made under normal conditions. Just as a "piano by virtue of its construction is capable of giving forth harmonies and discords which were not thought of when it was made, thus an organism, by virtue of its structure and peculiarities and the capacities conditioned by these, is able to carry through reactions, which normally do not take place, and which possibly never took place in its progenitors"[1]. If we wish to consider the reactions which occur during the formation of galls etc. as „abnormal combinations of normal components, yet we will not venture to compare among themselves the individual cells, of which the normal and abnormal tissues are composed, but must go further in our analysis and compare the individual partial processes by which the cells of the normal and abnormal tissues are produced. If we compare the cells as a whole with one another, we arrive at the conclusion that the organism is able to produce something "new". But if we keep to the individual partial processes, we recognize the fact that the "new" quality owes its origin to the same processes and same qualities of the cytoplasm as do normal elements. The localization, the intensity and the combination of these different partial processes can, however, occur very differently, according to the effective conditions and can produce very diverse products.

I believe that the contradiction in the statements of the authors above named may be thus explained:- We will have to express ourselves as for or against the production of "new" elements, according to whether we compare the complete cells with one another or fix our glance on the partial processes by which they are produced.

The individual partial processes making up the processes of formation of the different normal cells, can thus be so diversely combined that literally an unlimited number of cell and tissue forms can be produced. I call attention again to galls, especially prosoplasmas. The examples, described above, will have given already an idea of the wealth of their tissue forms. The diversity in the reactions of the cells and tissues corresponds to that in the combination of the effective factors, which likewise can be varied unlimitedly. We will not explain the distinguishable reactions existing in gall formations etc. by previous-
(293) xly fixed reaction mechanisms of which first one and then another is set in action, but by the varied combination of (internal and external) factors. The manner of action of each individual factor always remains the same in the same substratum, the diversity in the tissue products of the plant being explained by the peculiar combination of the different effective factors.

C. On the Capacity for Reaction

Almost all the processes in the living plant cell which are of interest to us presuppose primarily a definite nutritive condition, a definite degree of temperature, accessibility to air (oxygen) and the pressure of water. The cell becomes capable of reaction only through the fulfilling of these prescribed conditions.

We have already distinguished between a specific and an accidental inability to react - the accidental being conditioned by the energetic condition of the cells, the specific by the

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[1] Pfeffer, Pflanzenphysiologie, 2. Aufl., 1901, Bd. II, p. 171.

unchangeable peculiarities of their living cytoplasms. Accidental inability to react occurs when, at too low or too high temperatures, definite reactions of the plant are left out; - specific inability to react is shown by plant tissues when acted upon by magnetism and the like[1].

If we compare among themselves cells and tissues which are able to react we can easily prove that different kinds of cells respond to like stimuli with unlike reactions. Either only the intensity of the stimulatory effect is different, or the reactions also differ from one another qualitatively. If we compare cells of different plant specie s with one another, we may explain this different behavior partly by the specifically unlike conditions of their cytoplasms. If the cells of an organism or of an organ display differences in their ability to react, we may assume that the unlike conditions, to which the cells in the organism in correspondence with their course of development are exposed, may cause these differences. Dissimilar conditions not only have intensely influenced the cells in the course of their whole development, but still act upon them even
(294) at the moment of stimulation and during the reaction to the stimuli.

In the following, we will consider briefly the dissimilar behavior of different plants and tissues towards the same kinds of stimuli.

When comparing lower and higher plants with one another, cryptogams and phanerogams, we find that in all the arresting factors exercise about the same kind of effect. They are, however, unequally capable of reactions consisting of abnormal growth and abnormal tissue proliferations.

The scanty development of wound tissues in crytogams is especially striking. Indeed, cases are not lacking in which callus tissue is produced but no such extensive formations have been observed in them as are produced in phanerogams in the form of callus and wound-wood. In thallophytes, at times in algae and thalloid liverworts, when abnormal processes of growth are

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Our slight knowledge of the "internal" stimuli makes it very difficult for us to judge of ability to react and inability to do so. We will be able to trace back in many cases the omission of a reaction to the omission of some "internal" stimulus, as well as to explain them by (accidental or specific) inability to do so. A better insight is possible for us at present only in the cases, in which we have recognized definite reactions as caused by definite external factors. In many of the following statements, only future investigations will be able to decide, whether they are instructive on the ability of the cells to react, or rather on the causes of the stimulation. Also the distinction between accidental and specific inability to react can not be carried through in many cases. Hansen has shown that many yeasts lose their ability to form spores, when brought back into "favorable" conditions, may be cultivated further as "asporogenic races". If continuous, sporeless "races" are actually involved, it is a case in which "accidental" ability to react, caused by increase in temperature, becomes "specific" inability to do so, when the unfavorable life conditions are effective for any length of time.

called forth by injury, we find the production chiefly of normal tissue - proliferations of various kinds. In vascular cryptogams callus tissues are also rare. Fungi also seem very slothful to reaction.

No instance is known as yet in which cryptogams have produced hyperhydric tissues. Tyloses are rare in vascular cryptogams

Attention should also be called to the small part played by galls on the lower plants. Right here, however, we must refrain from abstract conclusions as to the cellular capacity for reaction, since like many others, the question has not yet been answered, as to how cryptogams react to the poison of gall insects which produce prosoplasmas and inhabit phanerogams if this poison is introduced artificially in the plants.

If Goebel[1], in his consideration of the formation of organs in plants, has arrived at the conclusion that lower plants, especially fungi, are more "plastic" for malformations than are higher plants, we can affirm in regard to the formation of tissue that higher plants are capable of greater production. Likewise, we find in phanerogams and especially dicotyledons the most extensive formations of tissue as well as the most abundantly and diversely differentiated ones.

If we compare tissues of different ages with one another, permanent tissues with young tissues, somatic with embryonic, we find that young tissue in many cases exceeds already differentiated or completely matured tissue in productive ability, but that, on the other hand, in many other cases, the cells of the permanent tissue have also retained their ability to react and can be incited to an extraordinarily lively formation of tissue.

The fact that the organisms which produce galls seek out young parts of the host plant, in order to incite these to gall formation, has often been treated and was mentioned above (p.227) (Thomas, Sachs and others). However, the conditions are not at
(295) all so simple as Sachs[2] assumes;- that gall formations are more abundant and more complicated, the younger the tissue from which they are produced. In many cases we findthat, just as richly differentiated abnormal excrescences are produced from tissue already differentiated - and still capable of growth - as from the tissue of the vegetative tip. Appel (loc. cit.) has tried to explain cases of this kind by the statement that in them the producer of the gall is able "to bring tissue already differentiated back to its original form, to make embryonic tissue from somatic", so that in the latter instance, embryonic tissue still produces the gall. I have already (loc. cit.) expressed my views against this theory and have referred to the fact that the embryonic tissue produced from the somatic under the influence of gall-stimulus represents in itself the young gall. With its production is proved the ability of the differentiated tissue to produce abnormal richly differentiated gall products from itself. In my opinion it would be absolutely unjustifiable to bring the differentiation of the gall products into interdependence with

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[1] Organographie, 1898, Bd. 1, p. 171.

[2] Physiol. Notizen. VII (Flora, 1893, Bd. LXXVII, p. 240).

the occurrence of the absence of a gall-plastein[1]. We find at times with the same kind of cell-division, the products of which may be called gall plastein, a production of highly differentiated galls and at times one of simple, homogeneous tissue excrescenses. The quality of the stimulus is the decisive factor.

I again call attention here to the bark gall of Chermas fagi, described by Hartig, which is likewise produced by abundunt tangential cell-divisions, as also the richly differentiated Banisteria gall, illustrated in Figure 93. The former arises partly from bark tissue which is several years old and thus furnishes proof that even mature tissue is still fit to produce galls. At any rate the Chermes gall here mentioned consists of the simplest, undifferentiated tissue, corresponding histologically to the callus excrescences produced after injury.

It must also be emphasized here, that gall formations are but little suited for a treatment of the question as to the distinct capacity of young and old tissues for reaction, since, for the present, in a decision as to the possibilities of the plant, we are dependent upon material present in nature and since no experimental treatment of the question has yet been successful. Since the gall insects always deposit their virus in the same kind of tissues, we can not find out how other tissues would act under similar treatment, i. e. after infection
(296) with the same poisons. The existence of any difference in principle between tissues of different ages, so far as their behavior toward chemical substances is concerned, is but little probable, since the cells even of permanent tissue several years old, like those of young tissue material, can be incited to similar or the same reaction to stimuli, by very different stimuli of some other kind.

Often cells of the permanent tissue are incited to abnormal growth and division by injury - instances of which are furnished by tyloses, and callus excrescences of the bark and pith. I may also call attention here to adventitious sprouts produced after injury on mature Begonia leaves. The ability to "restitute" tissue which has been lost by mutilation is possessed particularly by young tissues (compare chapter 1).

Kny has recently proved in Impatiens and others that the cells of the permanent tissue can also be incited to division by mechanical factors.

We find that hyperhydric phenomena of growth, occur in young bark cells as well as in those which are several years old. (Compare Chapter IV, 3).

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[1] Appel calls attention to the fact, "that gall formations can be produced in exactly the same stage on the same plant and yet their morphological significance may be very unequal. Thus the leaf louse Phyllapsis fagi produces simple warping and crumpling of the leaves, the Hormomyia species, on the contrary, structures of comparatively high differentiation. Both stimuli however, act in the same period, if not exactly at the same time; i. e. at the time of leaf distension. The difference consists in this, that the stimulus of the leaf lice encounters in this case mature tissue, which can not be transformed into one resembling plastein, the stimulus of the Hormomyia, however, is able to develop embryonic tissue, from which new tissue structures can be differentiated. (loc. cit.).

There remains finally a comparative consideration of the fate of the different tissue forms,- epidermis, ground tissue, vascular bundle tissue. In this we will limit ourselves to vascular plants. The above-said holds good so far as the utilization of galls in general conclusions is concerned.

1. Epidermis

The epidermis proves itself in general pretty resistant to arresting influences. In cultures in the dark, in moist places etc. its composition of histologically different elements remains approximately normal. To be sure pubescence is more or less reduced in the cultures mentioned, but the stomata are almost always retained. Gauchery proved in dwarfed plants, that the size of the epidermal cells remains normal in almost all of the species infestigated.

The epidermis is easily susceptible to favorable influences. It is possible, under very different kinds of cultural conditions to produce abnormally large epidermal cells. In cultures in moist places, after infection by fungi etc., we find a production of abnormally large epidermal cells- even the guard cells can attain an abnormal size (fig. 16). Callus hypertrophy of the epidermal cells, of which the guard cells are also capable, is illustrated in figure 28. Instances may also be found among intumescences in which the epidermal cells have become abnormally enlarged (Fig. 22). Especially interesting is the fate of the epidermal cells, which are incited by gall mites to hypertrophic growth, growing out to extensive, almost always unicellular pouches differently formed. (Figs. 38, 40).

When considering abnormal cell-division in the epidermis, we must distinguish between divisions perpendicular to the upper surface of the plant organ concerned, and those parallel to this surface.

In the production of many galls, we find that extensive excrescences arise by outgrowth of the ground tissues which are covered on all sides by epidermis. In this case, the epidermis (297) follows the growth of the gall-structure by repeated division perpendicular to the upper surface of the organ. It can not be stated definitely, whether the cells are incited to the processes of division only by passive distention or by the gall poison. That the epidermal cells are actually acted upon by the gall poison, however, and influenced by it, is proved by the abnormal hairs which often grow out of its cells at the infected spots[1].

Division parallel to the upper surface is rare. Only in a few galls do we find a many layered epidermis formed from the normal one-layered one (Spathegaster baccarum, Nematus etc.). Compare figures 98 and 99), and in some intumescences (see above). But even where cross-division does take place in the epidermal cells, it occurs less frequently than in the ground tissue cells belonging to it. The same holds good in the development of all callus formations. That epidermal cells may be incited correla-

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[1] In many cases, the epidermis is not able to follow the distension of the internal tissues by surface growth. I call attention to the gall of Hormomyia piligera (fig. 87) the Jacquinia gall (fig.101) and many intumescences (fig. 20).

tively to cross division, has not yet been observed[1].

It is possible that in the Marchantiaceae also a similar difference exists between the "epidermis" and the remaining tissue, as in the described higher plants. According to Vöchting[2] the "epidermis" in contrast to other tissue forms remains inactive in regenerative phenomena. Ruge[3] observed budding from the epidermis.

2. Ground Tissue

The ground tissue - the assimilatory as well as the mechanical, to name its two most important forms - is especially plastic.

Arresting influences of very different kinds are able to suppress more or less completely all processes of differentiation, to decrease the normal cell number and to prevent the full maturing of the indicidual cells (size, development, thickening of the membrane, formation of chlorophyll etc.). The cells of the ground tissue are shown to be in every way extraordinarily susceptible.

Favorable influences call forth in it hyperhydric, callus or gall hypertrophies in which, the cells of the ground tissue can grow out into great pouches and vesicles. So far as its capacityfor cell division is concerned, the gound tissue is greatly superior to the epidermis. Galls especially demonstrate that the cells of the mesophyll, of the bark etc. are capable of extensive division in all direc tions, the products of which can undergo most diverse differentiation. The ground tissue
(298) also participates greatly in the formation of callus tissues and is constantly livelier in its actionathan is the epidermis.

However, all the layers of the ground tissue in the same organ do not participate equally in the construction of abnormal outgrowths. In the window galls of the maple (fig. 42) the uppermost cells of the mesophyll often remain unchanged, while the cells of the other layer are greatly enlarged. The same holds good for the Banisteria gall illustrated in figure 93, in which the upper palisade layer remains normal, while the cells of the lower layers divide extraordinarily actively. In leaves infected by fungi, the cells of the spongy parenchyma are at times predominantly incited to division. In many other galls, the different layers of the mesophyll behave differently, yet the differences are not so strikingly noticeable as those in the cases first named (compare, for example, fig. 104). In intumescences the cells of the uppermost or undermost layer are often the only ones abnormally elongated, although we find in cases of "severe" sickness, that all the layers are similarly changed.

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[1] In the formation of adventitious shoots, cross-division takes place in the epidermis of various plants. As the best known example, the adventitious shoots of begonia leaves may be named here, which are known to be outgrowths of single epidermal cells.

[2] Ueb. d. Regeneration d. Marchantiaceen, Pringsheim's Jahrb. f. wiss. Bot. 1885, Bd. XVI, p. 367.

[3] Beitr. z. Kenntnis der Vegetationsorgane der Lebermoose, Flora 1893, Bd. LXXVII, p. 279.

3. Vascular-bundle Tissue.

The same plasticity exists in vascular bundle tissue, as in ground tissue.

To arresting influences of very different kinds, the plant reacts especially by the production of abnormally narrow ducts. It is known that under the action of continued and powerful disturbance, the normal composition of the xylem is lost, the libriform fibres disappear, ultimately the ducts also, resulting in a severe attack, in a completely homogeneous, parenchymatic tissue (callus tissue -gall wood). The phloem experiences a similar hypoplasia.

Favorable influences call forth abnormally large cells. We find that the bark grows out to hyperhydric tissues through the hypertrophy of its different elements, the wood-parenchyma cells form tyloses etc. or very extensive excrescences in the form of callus, wound-wood or galls are produced. In all essential points, the same holds good for this as for ground tissue.

Of the different parts of the cambium layer, that formed from the embryonic tissue, the cambium itself, is always capable of accomplishing the most. Yet even the tissue of the phloem, as shown above, can grow out into extensive callus robs or furnish large galls, rich in cells. The smallest part in the production of abnormal tissues is performed by the xylem, of which in fact the elements are mostly dead or lignified. Attention has already been called to tyloses. All other phenomena, known in the elements of the woody-part, play only a subordinate role.

If, after these brief discussions, we consider once more the different cell tissue forms arising during abnormal growth, (299) it may be affirmed, that the derivatives of very different kinds of tissues can assume very diverse forms. In the formation of galls true epidermis, bearing trichomes, can be produced from the mesophyll (compare for example, fig. 87), mighty sclereid complexas can be derived from the delicately walled mesophyll (fig. 90), true epidermis and typical ground tissue with stone cells can develop from mascular bundle tissue etc. in the formation of galls. - In the formation of callus, we find the production of derivatives of the pith, the secondary bark etc. and of tracheids etc. in short, from each tissue all can be formed, the course of their development is determined by the sum of all the factors acting on them. We find callus developing from the pith of wounded sprouts and the production in it of the same tracheal elements which under normal conditions are met with only in the xylem If in the interior of the normally developed shoot a cylinder of ground tissue is developed, instead of vascular bundle tissue containing tracheids, it is not due to any inherent peculiarities of the cells lying centrally, but is the result of all (internal and external) factors which have been active during the whole developmental period. Further, not only the cells of the dermatogen can develop "typical" epidermis bearing trichomes, but also; as proved by galls,- all other tissue forms. Further, the "normal" maturing of the ground tissue into assimilatory, palisade parenchyma, etc. is not a result of its specific constitution, which would permit of only one developmental course, but is conditioned by the factors, to the action of which the self-developing ground tissue is subjected under normal conditions. The fact that we always find the same tissues in the same order, in normally developed organs, proves nothing further than that in them the decisive active factors always come to expression in the same way.

Although all possible kinds of tissue can be produced from each kind, yet according to the present extent of our knowledge, a difference still exists betwenn the chief tissue forms in so far that the epidermis, as already stated, reacts with greater difficulty than the other forms of tissue and usually furnishes less numerous products during processes of division, while its dericatives do not seem capable of so extensive a differentiation as do those of ground tissue or of vascular bundle tissue[1]. Yet that the cells of the epidermis are able to produce all tissue forms from themselves, has been proved by the adventitious sprouts of Begonia leaves - to name only one example. These are known to develop from epidermal cells.

Therefore in plants, no such "specifioness of the tissue" exists as is usual in animal and human tissues. Do we find here a difference in principle between animal and vegetable tissues, or is the difference explained perhaps by the fact that the course of development of the animal tissues is determined chief-
(300) ly by "internal" factors and is not so actively influenced by a change of "external" factors, with which we work in any experiment, as is the course of development of vegetable tissue?

The knowledge that similar derivatives can be produced at different places, i. e. from different parts of the plant body, that, therefore, the capacities of the different plant tissues are fundamentally and everywhere the same forces as to the conclusion that, under normal as under abnormal conditions, the developmental fate of the cells and tissues in the last instance (within the possibilities of the plant) are determined only by the forces acting upon them, by the quality, intensity and combination etc. of these. From this point, we are led at once to new tasks and new discussions. When, in the formation of callus from pith and bark, or of galls from the derivatives of the ground tissue etc. the same vascular bundle elements are produced which usually in a normal course of tissue development occur in a circle around the medullary cylinder or among the cell elements furnished from the cambium, the question must be asked,- after we have recognized as impossible any specific cell-constitution,- whether, in the cases of normal and abnormal cell production here named, the same formative processes may always ib the last instance be traced to the action of the same factors. We must ask ourselves the same question, when the derivatives of the ground tissue and of the vascular bundle tissue grow out to just such epidermal cells and hairs as the elements of the dermatogen under normal conditions. The treatment of this and all similar questions which might lead to a developmental mechanics of plant tissues, has never been attempted as yet. It has already, however, become quite evident that no unsurmountable hinderances stand in the way of carrying out this treatment and many valuable results may be expected from it. I mean to discuss later in another connection the incentives to a treatment of developmental mechanical problems (here indicated) which the pathological anatomy of plants and especially the anatomy of galls, can give.

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[1] It should be noted here that the galls, to which we must refer first of all, have been by no means sufficiently investigated from histological and developmental points of view. Thus, for instance, developmental reports on the abundant gall-flora of North America are practically entirely lacking - the galls of Southern Europe have been investigated, at least predominantly as to their habitats and their most striking morphological peculiarities.- Perhaps I will succeed in inciting by these lines, new developmental studies, which, it must be stated, are urgently desired.

Remarks:

The German floral and animal (faunal) names are not given in the following index: also, with a few exceptions, only the generic names are given. Statements as to normal histological conditions have not been taken into consideration in the index.

Numerals refer to those in upper left hand corner of page. Marginal numerals in text refer to pages of German original.

The End.